

Proceedings of the American Academy of Arts and Sciences.

VOL. 57. No. 12.—JUNE, 1922.

CONTRIBUTION FROM THE CRYPTOGAMIC LABORATORIES OF
HARVARD UNIVERSITY.

LXXXIX. A REVISION OF THE ENDOGONEAE.

BY ROLAND THAXTER.

WITH FOUR PLATES.

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Received March 17, 1922.

Presented April 12, 1922.

IN preparing the present Contribution concerning the Endogoneae it has not been my intention to consider the subject in all its aspects, phylogenetic, cytological and other; and this revision has been undertaken chiefly with a view to the improvement of the systematic status of the family. For although relatively small, it has not escaped the taxonomic confusions and uncertainties which so frequently beset the path of the systematic mycologist, and it has seemed worth while to make at least an attempt to clear up some of the moot points relating to it, and at the same time to add such new information as I have been able to accumulate from personal observation or otherwise. I have therefore endeavored to obtain authentic information in regard to as many of the known forms as possible, and personally to examine as complete a representation of the type-material as could be assembled. Such value as this account possesses is therefore largely due to the courtesy of correspondents who have been so kind as to assist me in accomplishing these objects; and in this connection I desire to express my great obligation to Professor Abrams, of Leland Stanford, who has allowed me to examine all the Harkness types of Endogone in the University Herbarium: to the Abbé Bresadola, who has sent me a specimen of his *E. reniformis* collected by Rick in Brazil: to Dr. C. W. Dodge for Californian material collected by himself and by Mr. H. E. Parks: to Professor E. C. Jeffrey for a very interesting collection from Little Metis, Quebec, given to me many years ago: to Professor G. Lindau for the privilege of examining portions of all the types of Hennings and Bresadola in the Berlin Museum; to Mr. C. G. Lloyd for a portion of his *Endogone tuberculosa* and other interesting forms; to Professor O. Mattiolo who has sent me for examination specimens of all his material of Endogone, including the types of *E. Pampaloniiana* and *E. Tozziana*; to M. N. Patouillard for confirming my determination of his *E. lignicola* and for portions of the types of *Ackermannia*

Dussii and *A. coccogena*; to Professor Carlos Spegazzini for communicating the types of *Endogone fucgiana* and *E. argentina*; and to Miss E. A. Wakefield for opportunity to see Berkeley's types of *Endogone australis* and *Glaziella vesiculosa*.

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The fungi which are grouped in this assemblage of somewhat diverse forms are, in general, rather infrequently met with; owing in part to their apparent rarity, and partly to the fact that certain of the species, at least, are truly hypogaeous, and may develop at a depth of several inches below the ground, or beneath thick mats of *Sp hagna* or other mosses. While types of this sort are thus usually encountered by accident, or through the acquisition of what may be called a "hypogaeous instinct" which may enable one, after experience, to judge by various indications what situations are the most promising

for the collection of these and other fungi hypogaei, the recognition of others is surrounded by no such difficulty, since their fructifications may be developed free to the air, on mosses, rotten wood, leaves, dung or other substances above the leaf cover, or emerging from it.

It seems not improbable that the vegetative hyphae of all the Endogoneae are at first continuous. In a majority of cases, however, the hyphae of sporulating conditions show at least occasional septa, which, in highly developed sporocarps like that of *Glaziella*, become very abundant. The spores developed from these hyphae are either zygospores, thick-walled acrogenous chlamydospores or thin walled spores formed endogenously in sporangia.

The true relationships of the group to other families of fungi have long been a matter of conjecture, as is evident from the terms — asci, sporangia, cysts, vesicles etc.— which have been applied by various authors to the chlamydospores alone. But although the admirable researches of Bucholtz, who first (1912) published an account of its sexual reproduction, have thrown much needed light on its affinities, the group as a whole has been assumed to include forms of considerable diversity.

The inclusion in a single genus of the zygosporic and chlamydosporic types, has hitherto been based entirely on a general resemblance in habit and habitat, and a similarity in the appearance of the two types of spore, and there has been no evidence which would indicate that the two were ever produced simultaneously in the same sporocarp, or were closely associated in their natural habitats. This assumption proves, however, to have been justified; since in a single instance, among the northern forms collected by Professor Jeffrey and herewith described, zygospores and chlamydospores are so intimately associated in the same spore mass, that there can hardly be any question as to their specific identity.

Although the zygosporic or chlamydosporic nature of these spores is usually manifest, except in very old material, it is not always easy in cases where they are surrounded by densely compacted hyphal tissue, to determine whether their origin is sexual or not, the elements involved being so compressed and distorted that conjugating processes, unless very conspicuously differentiated, might well escape notice. This is true for example in *Endogone incrassata*, Figures 17–19, or *E. tuberculosa*. There seems, however, at least in the genus *Endogone*, to be a rather fundamental difference between the two types. In the zygospores, which are usually surrounded by a more or less definite hyphal envelope, an outer wall is present, within which a continuous

endospore is laid down, so that the contents is completely separated from the cavity of the origins. The contents is also more fatty and dense, often composed of distinct elements which may be very regular in size and shape (Fig. 9) and might even be mistaken for endospores.

The chlamydo-spores, on the other hand, although they may closely resemble the zygosporos, do not appear, as far as I have seen, to produce a continuous endospore; unless the otherwise anomalous *Glaziella* in which such an endospore is clearly distinguished (Fig. 91) proves to be an exception. For this reason, in a majority of species, the protoplasm of the chlamydo-spore and that of the sporophore are continuous, being connected by a protoplasmic isthmus which may remain unbroken even in mature spores (Fig. 46), or may be finally pinched off in the middle by the gradual thickening of the lateral walls. In a smaller number of instances, the separation between the cavities of the spore and sporophore is accomplished at an early stage through the formation of an independent septum, Figures 52-59 and Figure 85. Spores of the latter type have, for the most part, much thinner walls than those of the former, and were regarded by Bucholtz as perhaps young sporangia. An examination of various species and copious material, however, has convinced me that they are homologous with chlamydo-spores of the first mentioned type.

The so-called sporangia which have been above alluded to, Figures 60-78, which have been associated only with the genus *Endogone*, are quite unlike the other types of reproduction; and although I have followed previous writers by including them in this genus, there is no evidence beyond a certain resemblance between the sporangiocarp in the one case and the sporocarp in the other, which would tend to confirm the correctness of this reference. These sporangia are terminal vesicles, formed in a solid mass at the extremities of branching sparingly septate filaments which radiate more or less definitely from a cushion-like base. The spores which they contain are variable in size, form and number, thin-walled, with dense or fatty contents, and result from a total cleavage of the sporangial protoplasm. They are so characteristic that it would be quite impossible to mistake them for the spore-like masses above mentioned which may occur in zygosporos or sometimes even in chlamydo-spores.

Baccarini (1903) was of the opinion that these sporangial types should be removed from the *Endogoneae* and placed in the *Mortierelleae*; the sporangium in both cases being separated from the sporangio-phore by a simple septum. As Bucholtz remarks, this disposition appears to be somewhat premature. It must be confessed, however,

that if these sporangial forms are rightly included in the Endogoneae, it seems very probable that the two families should be regarded as very closely related, at least; since they are similar in two other important characters; namely, through the production of specialized zygosporic envelopes, and the presence of highly specialized acrogenous chlamydo-spores.

As far as I am aware, there has as yet been no successful attempt to germinate the spores of any of these fungi, or to grow them under artificial conditions; and in my own experience I have been unable, after repeated attempts, to induce the zygosporic forms of *Endogone pisi-formis* Lk. (*sphagnophila* Atk.) to germinate; or to procure any characteristic growth when uncontaminated spore-masses have been transferred to agar nutrients. The spore-masses of this species, when wintered over out of doors, have also failed to develop further. When placed on fresh sphagnum in a moist chamber for a protracted period during the summer, they usually become covered by a thin white coating of nondescript hyphae: but although various peculiar Zygomycetes, to which reference has been made in a former paper, (Thaxter (1897) p. 12) have at times been observed in such cultures, there is no reason to believe, even though, as in some instances, they seemed to grow from the masses themselves, that the association was other than an accidental one. It seems very probable that the thick-walled spores of the Endogoneae, as in various other instances, germinate as a rule only after special preparation, or under special conditions, and that in Nature they are eaten by various animals; continuing their development after being voided. This is suggested by the fact that I have myself observed uninjured spores of species of Endogone in the stomach-contents of shrews and of myriopods. Until successful cultures have been made, and the development of the three spore types has been successfully followed, or at least until more careful and extended field observations have given some evidence of their actual connection it cannot be assumed that they should all three be included within the limits of a single genus.

The literature of the Endogoneae, since the type species of the genus *Endogone* was described by Link in 1809, has been scattered and not very voluminous. With the exception of the paper by Buchholtz, above mentioned, and the enumerations in the Kryptogamenflora of Rabenhorst and of Cohn and the Pflanzenfamilien, there has, I think, been no general summary even of this genus. Von Höhnelt in his *Fragmenta*, Nos. VI, X and XV, discusses the synonymy and relationships of the genera *Endogone*, *Endogonella*, *Sclerocystis*,

Xenomyces, Ackermannia and Sphaerocreas; and numerous other references to the genus Endogone, or descriptions of new species, are to be found here and there in various other publications. In the appended list of literature, however, only such titles are included as are in some measure essential, and those which have reference merely to records of occurrence have been omitted.

Turning first to the genus Endogone, and following the conception of the genus which has been adopted by Bucholtz and all recent writers, one is forced to include in it all the three categories of spore-forms above enumerated, namely, zygosporoes, sporangia and chlamydo-spores. In order to avoid new names and combinations I have adopted this procedure as a provisional solution. It may be well to repeat, however, that although the sporangial forms arise in general from a similar vegetative body, and are associated in somewhat similar aggregations in similar habitats, their connection with the other types has not been definitely indicated, even by close association in nature, and their inclusion in the same genus is based on a pure assumption. Whether it may prove desirable to retain the name Endogone for the sexual and chlamydo-spore forms and to apply a different name to those which form sporangia is not as yet clear. It may further be pointed out that the presence of isogamy and of heterogamy, of specialized spore envelopes or their absence, as well as of simple and multiple aggregations of the zygosporoe masses, may similarly lead to a subdivision of the sexual forms themselves, under more than one designation. The desirability or the reverse of either of these procedures will, however, doubtless become more clear as the lacunae in our knowledge of the group are gradually filled.

The reasons which have determined the selection of the sexual forms as the true representatives of the genus, as originally founded, are based on an examination of the original figures and description given by Link (1808), of the type-species, *Endogone pisiformis*, on p. 33 of the apparently rare publication in which his paper is contained. The exact wording of this description is as follows:

“38. Endogone. Sporangium subglobosum, extus floccosum, intus grumosum sporangiola minuta, globosa, membranacea, sporidiis repleta.

“Præcedenti generi affine, (Tuber), supra terram in muscis crescit hypothallo radiciformi. Membrana externa sporangii tenuis floccosa. Contextus caeterum vesiculosus, microscopio simplici inspectus grumosus, at compositi ope conspiciuntur sporangiola, ut in præcedenti genere, dispersas inter vesiculos multo minores. Sporidia minuta, globosa, sporangiolis inclusa. Unica species.

"*E. pisiformis*, irregulariter globosum, lutescens membrana floccosa inductum. Magnitudine pisi. Fibrillis paucis muscis adnascitur in silvis abietinis. Membrana floccosa inducta tenuissima, sporangium intus colore lutescente Tuberis, at non venosum, sed grumoso granulolum. Segmenti transversalis particulam, V. fig. 52a, sporangiola cum sporidiis ibid. lit. b."

The figure "a" referred to, shows a portion of the spore-mass covered by a radiating sterile tomentum (membrana floccosa tenuissima) of tapering filaments, evidently more or less diagrammatically represented. The spores, which are shown embedded in the general mass (sporangium), are not subspherical, but more nearly elliptical, with the exception of those which may be assumed to be viewed end on. Figure "b" shows several of these spores (sporangiola) which have been forcibly and irregularly broken, as is evident from the rent through which the contents is represented as emerging. This contents is made up of granules indicated by single black dots, the "sporidia minuta" of the description, which bear no resemblance to resting spores and could not by any stretch of the imagination be regarded as intended to represent the large thin-walled spores of the sporangial type. This description is sufficiently clear, although, like most descriptions, incomplete, and taken in connection with the figures, which are not bad for the period, afford a reasonably satisfactory basis for determination.

Since *E. pisiformis* is the generic type, it is a matter of much importance to determine with some approach to accuracy, to which of the European forms now recognized it may be assumed to correspond.

Bucholtz, who may have seen transcriptions, only, of the original paper, and may have been misled by the confusing use of the terms sporangia sporangiola and sporidia, has assumed that the classic specimen collected near Naples by Vittadini and distributed in the *Fungi Europaei* No. 2516 under the name *Endogone microcarpa*, was to be regarded as the true *pisiformis*. It seems quite impossible, however, to reconcile the characters of the Vittadini form, which is the *Endogone malleola* of Harkness, with the account given by Link whose figures alone are sufficient to preclude the possibility of such a conclusion.

The more important points brought out by Link's account indicate that he was dealing with the type of sporocarp usually found in *Endogone*, consisting of yellow ellipsoidal thick walled spores with coarsely granular contents, associated with smaller vesicular structures, and irregularly disposed in a solid compact rounded mass surrounded by

a rather conspicuous "thin floccose membrane," and developed above ground on mosses.

If one compares with this account the characters of the other known European types, none seem to correspond so closely as *E. Ludwigii* Bucholtz (*E. sphagnophila* Atk.). No other species is found, as far as I am aware, growing on mosses above the surface of the ground, while its yellow ellipsoid spores with uniform coarse granular contents, and its conspicuous thin white superficial tomentum further distinguish it. The vesicular swellings of its hyphae, which are sometimes conspicuous among the larger spores, may further correspond to the "vesiculae multo minores" of Link.

Since for the reasons above indicated the reference by Bucholtz of *E. malleola* Hark. to *E. pisiformis* Link cannot be regarded as a possible solution of the difficulty, and since it is quite necessary to form some reasonably plausible opinion as to what constitutes the Type of the genus, I have felt it desirable to follow Krieger (1902) and the earlier opinion of Bucholtz, in referring to *E. pisiformis* Link the species more recently named by the latter (1912) *Endogone Ludwigii*.

ENDOGONE Lk.

Link (1809), p. 33.

Glomus Tulasne (1845), p. 63.

Hypogaeous or epigaeous: producing thick-walled isogamous or heterogamous zygospores with or without specialized envelopes: thick walled acrogenous non sexual chlamydospores: or thin-walled sporangia. The three types, as a rule, produced separately in compact groups, which may be single or associated in a common mass, naked or surrounded by a variably developed pseudoperidium or tomentum, and may form either a definite sporocarp or an indefinite loosely coherent spore-mass.

Type Species.

ENDOGONE PISIFORMIS Link.

(Figs. 1-7.)

Link (1809), p. 33, Taf. II, fig. 52, a & b. Bucholtz (1902), p. 81, Tab. II, fig. 13 and V, fig. 4.

Krieger (1902), Fungi Saxonici, No. 1651.

Endogone Ludwigii Bucholtz (1911), p. 194, Taf. IX, figs. 77-87.

E. sphagnophila Atkinson (1918), p. 16.

E. xylogena Schroeter (1887), p. 260, *nec.* Saccardo (1877), p. 14, sub *Protomyces*. Thaxter (1897), p. 12.

Spore-masses waxy when fresh, horny when dry, pale to golden yellow, becoming somewhat orange yellow, subspherical to reniform, or lobed, less often convolute, flattened, umbilicate below: covered by a thin tomentum, clear white when dry, formed by characteristic, thick-walled hyphae 4-6 μ in diameter with numerous free, projecting, distally attenuated branches. The substance of the spore mass consisting of an irregular plexus of stout branching non-septate filaments, showing numerous irregular vesicular enlargements, becoming more or less obliterated as the irregularly crowded, broadly ellipsoid to ovoid, thick-walled, pale orange yellow zygospores mature. Spore-masses (dry) 2-7 \times 1-2 mm. thick. Zygospores, 35-60 \times 30-45 μ , the wall subhyaline 3-5.5 μ thick. Peridial hyphae \times 3-8 μ .

Usually above, rarely below the leaf cover; on mosses, especially near the tip of Sphagnum; on leaves, twigs, dung, rotten logs, etc., in moist situations, especially in coniferous woods. Temperate Europe and North America.

This species is without doubt very generally distributed in temperate America; since it is already known to occur in Maine, New Hampshire, Connecticut and eastern Tennessee (Thaxter); West Virginia (Sturgis); New York and Maryland (Atkinson), and in Michigan (Kauffman). In my own experience it has proved not at all uncommon, and was first met with at Kittery Point, Maine, in 1886, when young conditions, showing the early stages of conjugation were obtained. Although it is found most frequently at or near the tips of Sphagnum, especially in moist coniferous woods, and is conspicuous in this position from its bright color, it bears no definite relation to this substratum as a host; since it occurs also, as above indicated, on various other substances. Its waxy consistency, when fresh is, as noted by Schroeter, characteristic; as is the hard almost horny character of the dry spore mass, which loses its bright color, becoming dirty yellowish; the variably developed superficial tomentum assuming a more noticeable clear white appearance, owing probably to the refractive character of the thick walled filaments which compose it. The size and form of the spore-mass varies considerably from nearly round to flattened and somewhat convolute. The largest individual seen measures 7 mm. in width when dry.

The early conditions of development are much more difficult to

detect, from their small size and much paler color. The process of conjugation is not progressive in the developing mass; but occurs almost simultaneously throughout it, the rather rapid enlargement of the whole being due to the simultaneous increase in size of the individual zygospores. The gametes are subequal, and do not differ from one another more than is frequently the case in other isogamous types. They are subcylindrical and lie parallel to one another, distinguished by a clean cut septum at some distance below their adherent tips, Figure 1. The developing zygospore rises from this point of contact, above and between the extremities of the gametes, Figures 2-6. The successive stages in this process are not unlike those figured by Van Tieghem (1873), Pl. III, figs. 88-93, in *Synecephalis cornu*.

Before full maturity, the hyphal elements of the mass are conspicuous, and rather characteristic from their large size, their branching and the development of vesicular swellings which I have assumed to be the "vesiculi multo minores" mentioned by Link, and which are referred to by Bucholtz as "stellenweise verbreiterungen." As the zygospores mature, these elements become compressed between them, and may be hardly recognizable, their flattened remnants forming, in many cases, an irregular envelope about the individual spores.

The branching terminations of the filaments which form the superficial tomentum are well figured by Bucholtz (1911), fig. 77, and possess great individuality, Figure 7, but are not always conspicuous in older individuals. The prominence of this tomentum varies greatly in different individual masses, and under different conditions. It seldom seems to be so copiously developed as is represented in the figure of Link, which is evidently somewhat diagrammatic, and in older specimens may appear to form a rather even covering of apparently nearly uniform elements.

The description given by Schroeter of *Endogone xylogena* corresponds so closely to this species, that I have included it as a synonym. It seems quite improbable that the plant which he examined could have been the *Protomyces xylogenus* of Saccardo; since the latter is without hyphae, and corresponds in all respects to the sclerotium-condition, "Phylloedia," of some myxomycete: its habitat, buried in soft rotten wood and exposed only by the weathering of the latter; its yellow color, and the general appearance of its spores, being the same. The figures given by Saccardo (1877) in the *Fungi Italici*, fig. 104, show the somewhat irregular outline and the characteristically thickened, but ill defined, walls of this well-known condition of the myxomycete plasmodium.

With reference to the occurrence of this species in Europe, it may be mentioned that the single specimen collected by Bucholtz in Livonia was found "in einem nadelwald unterirdisch," and was associated with insect-remains, which suggests that it may have grown on the dung of some small animal, a habitat which I have myself observed. The apparently copious material collected in Thuringia by Ludwig, which forms the basis of the account given by Bucholtz, was found on the dung of *Liparis* caterpillars. The specimens distributed by Krieger were found "Auf Moos, faulenden Blättern, Aestchen, unter Strauchern von *Vaccinium myrtillus* auf dem Fichtelberge in Erzgebirge."

With regard to mutual identities in connection with this species, it should perhaps be clearly stated that while the use of the name *E. pisiiformis* and the inclusion of *E. xylogena* as a synonym represent merely my personal conclusions, Professors Atkinson and Bucholtz have both examined the material on which the present account is based, and have pronounced it identical with *E. sphagnophila* in the one case, and *E. Ludwigi* in the other. It may further be mentioned that one of the specimens distributed by Krieger, has been examined by me personally, and is also identical; although a second specimen in the same copy of this set, the gross appearance of which is very similar, proves to be *Sphaeroceas pubescens*. As it is stated that the fungus was found "sehr selten," it may be assumed that the distribution is a miscellaneous one, accumulated from more than one gathering. The possible relation between *Sphaeroceas pubescens* and *Endogone pisiiformis* will be further alluded to under the former species.

For convenient comparison, the description of *E. xylogena* given by Schroeter (l. c.) may be here appended.

"*Endogone xylogena* (Saccardo (1877): *Protomyces* x.). Fruiting bodies irregularly rounded, flattened, 3-4 mm. broad, 1-2 mm. thick, waxy when fresh, horny when dry, reddish yellow. Peridium thin, formed from 3-5 μ thick, strongly refractive hyphae, smooth. Gleba homogeneous, consisting of closely woven hyphae between which the spores are disposed. Spores spherical to elliptical or ovoid, 35-50 \times 26-40 μ , the wall 6 μ thick, nearly hyaline, contents clear orange yellow.

***Endogone multiplex* nov. sp.**

(Figs. 8-10.)

Fruiting body about 15 \times 12 μ m., dirty whitish, turning yellowish brown in alcohol; somewhat lobed, the surface rough from the projecting contours of the very numerous small, more or less firmly

coherent, rounded or somewhat irregular spore-aggregates, of which the mass as a whole is composed, and throughout which a large amount of finely divided humus material is incorporated. Individual spore-groups more or less rounded, or somewhat irregular, mutually coherent, or readily separable, 350–700 μ in diameter, and including from ten to fifty spores each, more or less; each group surrounded by an envelope of hyphae among which a considerable amount of humus material is incorporated; the hyphae variable in diameter, 4–18 μ , thick-walled, rather brittle, freely branched, three or sometimes four branches often radiating from subtriangular or angular enlargements, especially in the larger ones, which are rather conspicuously distinguished, though scanty. Zygosporcs yellow, spherical, oblong to ovoid or piriform, often irregularly subangular from pressure, 80–90 \times 60–84 μ ; the endospore clearly defined, slightly yellowish, about 5 μ ; the exospore hyaline and, when freed, swelling to 8–10 μ ; the contents rather bright yellow, composed of nearly spherical fatty bodies 4–8 μ in diameter which completely fill the cavity. The attachments of the suspensors clearly defined, sometimes approximated, more often distant: the spore surrounded by a clearly defined, relatively thick, separable envelope, 8–12 μ thick, of closely felted hyphae.

Growing beneath the leaf cover beside a path in mixed deciduous woods (oak and hickory) on Cutts Island, Kittery Point, Maine: September 15, 1902.

This species is most nearly related to *E. tuberculosa*, but differs in various essential points. The individual spore-masses are, as a rule, very readily separable, so that a small fragment of the fruiting body, when teased or rubbed under the cover glass, separates to a mass of rather uniform coarse granules, which represent the individual spore-groups, Figure 10: the envelopes of which are composed largely of humus particles which often wholly conceal the spores within.

The material is unfortunately fully matured, and it is thus impossible to determine the exact nature of the process of conjugation, and even the suspensors are for the most part disorganized to such an extent that their form and limits can no longer be made out. The relation and attachment of the latter to the spore are very characteristic. They are always quite distinct, Figures 8–9, sometimes close together, but usually separated by a considerable interval; in this respect recalling the similar relation so often seen in the zygosporcs of *Choanephora*. On treatment with potash, the separable exospore and the surrounding filaments become considerably swollen and gelatinous, so that their limits are determined with difficulty.

The peculiar characters of this species illustrate the culmination of the tendency toward a definite grouping of the spores within the gleba, which is present to a less marked degree in *E. tuberculosa* and *E. fuegiana*. The sexual nature of the spore-origin is unquestionable from the two distinct origins are present in all spores. The alternative that they may be intercalary and represent a lateral bulging, so to speak, in the continuity of the hypha, is an explanation which is rendered quite improbable by our knowledge of spore-formation in all the chlamydosporic types. The conjugation is evidently somewhat peculiar, as is evidenced by the often remote origins, and it is to be regretted that, owing to the fact that the whole spore-mass is hardly distinguishable from a slightly coherent mass of earth, the younger stages are not likely to be found, unless by accident.

ENDOGONE TUBERCULOSA Lloyd.

(Figs. 11-16.)

Lloyd (1918), p. 799; fig. 1239.

This species has been described and its gross appearance well illustrated by Lloyd, to whom the writer is indebted for a small portion of the type material on which the following notes are based. It was collected in New South Wales by Mr. J. B. Cleland, who states that it was found just at the surface of the ground, apparently partly buried in it, if one may judge by the coating of earth which completely envelopes it. Its gross characters are peculiar from the fact that the gleba is not a continuous and undifferentiated spore-mass, but is in a sense compound.

The sporogenous area, which is only visible in sections, Figure 11, is very irregular in outline, pushing indeterminate lobes or extensions outward into the surrounding covering of earth, which thus varies greatly in thickness, and appears to be held together by a scanty penetrating mycelium. It is possible, after slightly moistening the cut surface, to determine that the golden yellow spores are arranged in rounded masses of variable size and shape, or are associated in larger somewhat less definite areas. In either case they are often, though not always, separated by intruding layers of the earthy matrix, the presence of which is indicated by its darker color, and which may be even more intimately incorporated in the general mass, although none appears to occur within the individual spore-groups.

In these spore-groups, or areas, the more clearly defined of which

may be from 350–1000 μ in diameter, more or less, the bright yellow spores are closely packed and coherent, each surrounded by a thin, but as a rule clearly defined, envelope of closely matted finer hyphae. Penetrating the larger groups or areas, or separating the smaller ones,¹ vein-like wefts of coarser filaments, forming an irregular pseudo-parenchyma, may be present, Figure 12, so that the general appearance of the cut surface is not unlike that of one of the Tuberaeae.

The individual spores, Figures 12–16, are often irregular from pressure, and very variable in size and outline; subspherical or more often longer than broad, elliptical, subpiriform or often elongate, 50×42 – $150 \times 90 \mu$, the average about $90 \times 65 \mu$; the exospores about 5–6 μ , becoming very thick, even 15 μ ; the endospore comparatively thin, about 1–2 μ . The yellow contents consists of not always dense, granular fatty protoplasm, usually associated with larger fatty masses or globules; but in certain fully mature individuals, it appears to have lost its color, becoming hyaline; while the exospore is greatly thickened, Figure 14, intruding irregularly, somewhat as in *E. incrassata*, and throwing the endospore into irregular folds.

Although, owing to the mature condition of the specimen, the spore-origins are for the most part shriveled or destroyed when freed from the tenaciously adherent spore-envelopes, a sufficient number have been isolated to satisfy me that two hyphal elements are involved in spore-production, which are associated and differentiated much as in *E. lactiflua*; although relatively smaller and less conspicuously different, one from the other, than in this species. In one instance, only, Figure 13, has it been possible to determine with some exactness the more normal appearance and relation of the two conjugating elements, although many have been observed in which the remains of corresponding structures were clearly traceable.

In the type figured by Lloyd, the surface of the specimen is considerably and irregularly roughened, pitted or lobed, the roughness having apparently suggested the specific name. This tuberculate habit does not, however, appear to be related to the presence of the characteristic spore-groups, and is merely a modification of the earthy covering.

The species is more like *E. pisiformis* in the form and color of its spores, but resembles *E. lactiflua* in its type of conjugation. In the grouping of its spores and its yellow color it recalls *E. multiplex*, which is nevertheless readily distinguished by the two discrete suspensor-insertions which characterize this species. The grouping of the spores is similar to that found in *E. fucigiana*, which, however, forms

a compact continuous spore-mass, without incorporated foreign material, and in which the origin of the spores and spore-groups is quite different and apparently non-sexual.

Endogone incrassata nov. sp.

(Figs. 17-19.)

Fruiting body even or somewhat lobed, yellowish, with a whitish scaly or reticulate crust variably developed, about 2-5 mm. in diameter when dry. Gleba firm and compact, yellowish; the hyphae thin-walled and vesicular, or running in strands or bundles between the spores; the thin peridial region of more slender thick-walled filaments. Spores scattered thickly, without definite arrangement, throughout the mass of the gleba, which contains no foreign matter; more nearly isodiametric, somewhat irregular in outline, subspherical to broadly oblong, at first filled with rather uniform yellow subspherical fatty granules, about 3-5 μ , the continuous endospore clearly defined, thinner than the exospore; the two about 8 μ thick; the exospore becoming much thickened, 16-20 μ , intruded toward the center and pushing the endospore into folds, the contents losing its color and granular character. The spores 66 \times 64-75 \times 85 μ .

Under spruce, about two inches below the surface of the cover; with a distinct alliaceous odor. Gerrish Island, Kittery Point, Maine; August, 1896.

Three specimens of this species were found associated, and close by a single individual of *E. radiata*, of which it may possibly prove the sexual form. The gleba is so dense, and its elements surrounding the spores so vesicular, that it has been impossible to make out with certainty the character of the gametes which are evidently small, not clearly distinguished and almost obliterated by the enlargement of the spores and the consequent pressure. In a few instances, appearances have been seen such as are represented in Figures 18-19; but, in the dense pseudotissue about the spore, it is quite possible that the apparent conjugating spore-origin may be in reality due to an accidental juxtaposition of gleba elements, bearing a superficial resemblance to conjugating structures.

The spores when fully matured, Figure 19, resemble those of *E. tuberculosa*, Figure 14, although the wall of the exospore becomes relatively thicker and the endospore is thrown into deeper and more complicated folds by its intrusion. In this condition it is quite hya-

line and impenetrable by stains, the contents losing its granular character entirely. The spore-envelope is thin and not clearly differentiated. The scaly or flecked appearance of the surface of the sporocarp is due to patches of loose hyphae which project from the peridium, and in section appear as flat tufts.

ENDOGONE LACTIFLUA Berkeley (1846).

(Fig. 20.)

Berkeley (1846), p. 81. Tulasne (1862), p. 183. Bucholtz (1912), p. 155, figs. 1-61.

Endogone lanata Harkness (1899), p. 280.

This species has become for the first time thoroughly well known through the researches of Bucholtz, who was not only the first to see and to describe the sexual origin of its spores, but to figure clearly the remarkable envelope which surrounds them at maturity, formed from labyrinthine filaments which eventually become thickened and modified to form what he has called a "flammenkrone," which is firmly adherent to the exospore. Both the envelope and the flammenkrone, however, vary, as is mentioned by Bucholtz, (1912), p. 165, in different individuals, apparently according to the age of the spore-mass, and in some of the Hesse specimens in the Farlow Herbarium neither are striking or easily recognized; while in others they are apparent at a glance. The same is true of material which the writer has collected at various times and in various localities in New England; at South Billerica, Mass.; at Kittery Point, Maine, where seven different gatherings were made; and at Intervale, New Hampshire. In all these gatherings, which were mostly of single specimens, the gross size is smaller and the spores themselves larger than in the Hesse specimens; and while in some the labyrinthine envelope-filaments (Bucholtz, fig. 50), though finer, are quite as distinct and the flammenkrone clearly distinguished, in a majority of cases these structures are not clearly visible, except that a well developed hyphal sheath is always present. Entirely similar conditions are, however, seen in some of the Hesse specimens, so that it seems probable that their distinctness may be a matter of age or some of the circumstances associated with their growth. Although in the Hesse material the spores are usually only 100 μ in diameter, while in the American they

are 120–125 μ , specimens received from Hesse by Ed. Fischer are reported to be 115–125 \times 70–90 μ , and in the large number of cases reported by Bucholtz, the range of variation is 68–160 \times 60–104 μ . The discrepancy is thus not so great as it might at first appear; although further examination may indicate that more than one specific form is represented in this series.

Although the occurrence of this species in America has not been hitherto recorded, it appears to have been collected several times by Harkness in California. Through the courtesy of Professor Abrams of the Leland Stanford Herbarium, I have had an opportunity to examine all the material of *Endogone* referred to by Harkness, (1899), in his paper on Californian Hypogaeous Fungi, including "*E. lanata*" sp. nov., "*E. microcarpa*" Tul. and "*E. macrocarpa*" Tul. The portions of these specimens communicated are similar in color and appearance, and it would be impossible to distinguish either of them by their microscopic characters from the eastern material above referred to. In all, the conjugating processes are clearly defined, and the spore-envelope well developed. In the specimen marked "*E. macrocarpa*" this is especially true, the flammenkrone, though not as striking as in the best developed Hesse specimens, being clearly present. The size of the spores in these Californian specimens is also similar, the longer axis varying from 125 μ or less to 160 μ : a range similar to that reported for the European types.

In a single specimen found at Kittery under beech trees, the gleba is dark blackish brown, the color being apparently due to the fact that a large amount of finely divided humus material is incorporated throughout its substance, a condition seen elsewhere in *E. multiplex* and a few other species. The zygosporangia differ somewhat in possessing a somewhat roughened, smoky brown exospore, distinctly unlike the yellowish wall of the ordinary type. It has not seemed desirable to separate this form specifically, however, on the basis of a single specimen.

For further details in regard to *E. lactiflua*, the admirable and very complete account of Bucholtz should be consulted. The possibility should be borne in mind that the very variable series of forms now included under this name may prove to represent more than one species, when they become more thoroughly known, and their life-histories have been traced. In the present state of our knowledge, however, the use of a single name to designate them seems in every way desirable.

Endogone fasciculata nov. sp.

(Figs. 21-28.)

Spore-masses spongy, loosely coherent, rather thin and irregularly lobed, somewhat amorphous, 10-14 × 4-5 mm., but very variable, incorporating more or less of the substratum (*Sphagnum*) and other foreign matter. Chlamydospores in rounded or somewhat elongate or irregular coherent groups, associated with less definitely distinguished masses of readily separable zygosporae; pale yellowish or faintly brownish, mostly spherical or somewhat longer than broad, 60 × 60-85 × 70 μ, the wall becoming relatively very thick, 6-10 μ. Zygosporae immature, irregularly spherical, colorless, about 50 μ, arising from the larger of two unequal gametes.

In *Sphagnum*. Little Metis, P.Q. E. C. Jeffrey.

This species is in some respects the most interesting member of the genus, since it is not only peculiar from the grouping of its spores, but presents the only instance in which zygosporae and chlamydospores have been found intimately associated in the same spore-mass. It thus furnishes the first indubitable evidence that the zygosporic and chlamydosporic types have been rightly included in a single genus.

None of the zygosporae examined are mature, but there is no indication that any special envelope is developed about them, as in *E. lactiflua* and some other sexual forms; although the process of formation, Figures 23-26, is very similar to that which occurs in the last mentioned species. The hyphae with which they are associated are thin-walled, scanty and evanescent; so that even in the youngest stages of conjugation, the exact origin and relation of the progametes is not clearly evident. Although this cannot be regarded as determined beyond question, examination of young stages under an immersion seems to show that the type of conjugation is homothallic, and that the progametes arise in proximity to one another from the same filament. The gametes are distinguished much as in *E. lactiflua*, one being larger than the other, and bearing the zygosporae, which bulges upward; both remaining attached, with slightly thickened walls and septa. The groups of zygosporae are more irregular and undifferentiated than those of the chlamydospores, among which they are irregularly distributed in continuous masses.

The chlamydospores arise from a plexus of clearly defined, thick-walled, variously bent and interlaced branching hyphae, which form a core from which short irregular sporiferous branches grow radially

outward. The chlamydo-spores are thus at first rather firmly associated in grape-like clusters, which may be of definite rounded outline, Figure 21, or longer or more irregular. This definite relation seems to be more or less obscured in older specimens in which the hyphae tend to break up, as in other species of the genus. It should be mentioned that zygo-spores do not seem to be invariably associated with the chlamydo-spore form. The chlamydo-spores themselves are rather uniform, commonly more or less spherical or but slightly longer than broad, and when fully mature possess a relatively very thick wall, surrounding a coarsely fatty contents.

The species is most nearly related to *E. vesiculifera*, which seems very clearly distinguished by the peculiar clavate empty vesicles which are associated with the chlamydo-spores. In the grouping of its spores it also bears some resemblance to *E. fuegiana*, which is at once distinguished by its hard continuous gleba.

Endogone vesiculifera nov. sp.

(Figs. 29-32.)

Spore-mass loose in texture and without definite form, about 5-8 × 4 mm., incorporating more or less of the substratum (Sphagnum) and some other foreign matter. Chlamydo-spores arising in groups, rounded or more elongate, often not clearly defined; pale yellowish, spherical or slightly longer than broad, rather uniform, about 65 × 65 μ , the larger 80 × 70 μ : arising from fascicles of intricately woven, branching, thick walled hyphae, and borne terminally on short radiating branches; associated with broadly clavate vesicular cells, 100-125 × 50-64 μ , which extend outward beyond them.

In Sphagnum, Little Metis, P.Q. E. C. Jeffrey.

The material of this form is somewhat scanty, although sections of three different individuals are preserved. It resembles *E. fasciculata* very closely, the chlamydo-spores being very similar in size and shape and similarly grouped about a core of thick-walled hyphae. It is readily distinguished, however, by the presence of numerous pear-shaped or broadly clavate, nearly empty, thin-walled, sterile vesicular structures which arise in company with the chlamydo-spores from slender short branchlets. These bodies are very characteristic, and although their origin is the same, are by no means ordinary chlamydo-spores which have failed to develop. They are no doubt the homologues of spores, but cannot be directly compared with the numerous

empty abortive vesicle-like spores which are conspicuous, for example in *E. canadensis*. In many cases their broad projecting terminations form a continuous margin about the spore-groups. Those of the latter which are peripheral, may be further enveloped externally by a closely woven layer of fine, thin-walled, hyphae, which may penetrate inward to some extent, between the vesicles and spore-groups, entering the spores themselves and filling them more or less completely. This parasite seems similar to that which attacks *E. lactiflua*, *E. fuegiana* and other species.

ENDOGONE FUEGIANA Spegazzini.

(Figs. 33-34.)

Spegazzini (1887a), p. 6, No. 5; (1887b), p. 120.

Through the courtesy of Professor Spegazzini I have had an opportunity to examine the type of this species collected on Staten Island, Straits of Magellan. In its present condition the type does not show all the characters mentioned in the original description which, since the publication in which it appeared is rare, should perhaps be quoted in extenso.

"Globoso vel elliptico repanda, extus alba, levis vel vix sub lente valida flocculosa, parvula (2-5 mm. diam.), inferne saepius umbilicata vel depresso-rugulosa centroque nodulosa vel subcicatricosa, uda compactiuscula tenacella; sicca dura, fere cornea: cutis carne arcte adnata persistens; caro sordide alba sub sectione fulvo-maculata, ob punctulos rufos dense congestos: puncti 7-8 cellulares, globoso sub-polygoni (180 μ diam.), carne innati, nunquam confluentes: cellulae punctulorum sphaeroideae e mutuo pressione saepius ovoideae (80 \times 65 μ) laeves, crasse tunicatae ad verticem praecipue, inferne subapiculatae ac nodulo majusculo obscuriore donatae, fulvae vel subtestaceae. Inodora, insipida."

Found under moss on Staten and Clarence Islands, Straits of Magellan.

There has been some question as to the true position of this species, owing to the characteristic arrangement of its spores, the "cellulae" of the above description, which are more or less definitely and compactly associated in small groups of six or usually more, Figure 33, separated by variably distinct strands of compact parallel hyphae, an arrangement which gives an irregular and rather faintly areolate appearance to sections of the gleba. This has led to the suggestion that the plant might be an immature condition of some tuberaceous

form. The species is, however, a well defined Endogone. The spore-groups are smaller and more clearly defined than those of *E. tuberculosa*. Spegazzini remarks that the spore-groups are never confluent; but a section from the dried material shows that they are not always distinguished with great clearness, and are at least often in close contact.

The spores, unlike those of *E. tuberculosa*, are reddish brown, considerably smaller and more nearly spherical, though usually irregular from mutual pressure. Their greatest diameter seldom exceeds 80 μ , while that of *E. tuberculosa* is often as much as 125 μ . The gleba is a dirty brownish yellow with a reddish tinge, horny when dry, the strand which separates the spore-groups, which are not always clearly marked, having a darker brownish color. The gleba, unlike that of *E. tuberculosa*, is continuous in the sense that, as far as I have seen, it contains no incorporated foreign matter.

The origin of the spore-groups is quite remarkable, and I have had some difficulty in making it out, owing to the scantiness of the material which it was essential to injure as little as possible. Their origin seems unassociated with any sexual process, and careful examination of a section shows that the spores, which are practically sessile, originate by budding in all directions from an enlarged hyphal termination. In the fully mature condition which characterizes the type, this termination is very thick-walled and irregular in outline. At points where a spore-group has been cut nearly through the middle, one may see sections of these thick-walled terminations with one or more definitely related spores in situ, as indicated in Figure 34. Each termination appears to produce as many spores as can be crowded around it, and when the group is viewed from without, it is quite impossible to see any indication of their mode of origin. Although a multiple origin of zygospores from a single conjugation is not necessarily excluded as a possibility in this instance, and might find a certain analogy among the Entomophthorales where two distinct zygospores may be produced in this manner, it may be assumed that the process in this instance is purely asexual and that it is merely a more specialized manifestation of that which occurs in *E. fasciculata*, in which, owing to the loose texture of the general mass, the spores, although arising in crowded groups, are produced in a more nearly normal fashion. This conclusion is further supported by the structure of the individual spores which lack a continuous endospore. A majority of the spores are attacked by a sterile parasite similar to that mentioned in the preceding species and shown in the spore at the right in Figure 34.

ENDOGONE MACROCARPA Tul.

Tulasne (1851), p. 182, Pl. XX, fig. 1. Bucholtz (1912), p. 184, figs. 62-74.

Nec Harkness (1889), p. 279.

Glomus macrocarpus Tul. (1845), p. 63.

Endogone australis Berk. (1860), p. 270.

Bucholtz (1912) gives an extended summary of the occurrence and spore-variation in this species, which indicates that it is perhaps the most frequently observed and variable member of the genus. The only records of its occurrence in America are that of Lloyd (1908), who reports it somewhat doubtfully from the Bahamas; and that of Harkness (1899) who speaks of finding it under *Libocedrus* at Towles, in the Sierra Nevada Mountains, California. Mr. Lloyd informs me that the Bahama specimen, which was doubtful, and may have been *E. fulva*, has been lost; so that this record must remain very dubious. The California form, which I have examined, proves, as above stated, to be *E. lactiflua* and is identical with what I have called by this name from the East. The spores are clearly zygospores, and the hyphal envelope is well developed, although the "flammenkrone" are not so strikingly differentiated as in some of the Hesse specimens, in the Farlow Herbarium.

In New England I first encountered what I have regarded as this species, growing on earth in greenhouse pots at the Botanic Garden in Cambridge, in company with *Hymenogaster Klotschii* and *Hydnangium carneum*, a habitat and association which has also been noticed in Europe. Of this material, one gathering made in the winter of 1891-92, has spores seldom exceeding 100 μ in greatest diameter, while a second gathering made two years later from the same pots, has spore-masses in which the larger spores measure from 170-200 μ in greatest diameter. In neither of these was any definite peridium developed, possibly owing to the fact that both grew on the surface and were subjected to constant watering.

In addition to these two gatherings, seven others have been made at Kittery Point, Maine. In these instances the fungus was found in moist coniferous and deciduous woods, usually just below the leaf cover rarely on the surface; the spore-masses usually solitary, or but two or three together. This material also shows a considerable range of variation in the size of the spores; although a majority correspond in this respect to the first gathering above mentioned. The larger spores are in general 80-100 μ in greatest diameter. This average maximum

is considerably below that given by Bucholtz in his summary of the spore measurements of twenty-seven European gatherings; which includes no case in which the maximum is below 100 μ . When one considers, however, that he gives a variation of the maximum diameter in this summary between 112 μ and 230 μ , the smaller maximum of the American material does not appear significant.

The structure and character of the gleba is also subject to variation which bears no evident relation to the size of the spores. The hyphal matrix is thus quite loose in some individuals, and the spore origins correspondingly conspicuous; while in others it is as densely compacted as in *E. lactiflua*, so that clearly recognizable spore-origins, though readily made out, have to be sought for. Although Baccarini (1903) has made this difference a basis for the separation of his *E. Pampalomanana* (vide infra), it hardly seems a sufficient specific distinction.

Through the kindness of Dr. Dodge, I have had an opportunity to examine three gatherings made by Mr. H. E. Parks in California: No. 348 at Saratoga, No. 312 at Aldercroft Creek, and the third at Guadalupe. All of these are unusually well developed. The largest measures 15 mm. dry: the peridium is unusually thick, yellowish white, with adherent humus material. The gleba is firm and dull yellowish in the dry material, although dark brown in the alcoholic specimens. The nearly spherical spores often reach the maximum of 230 μ mentioned by Bucholtz, and the wall, which may reach a thickness of 18 μ , is traversed by radial canals (?) which, although they are much less strikingly developed in a few other specimens examined in which the walls are unusually thick, are here very numerous and conspicuous, and appear to be associated directly with flattened masses of oily material which adhere to the inner surface, and from the middle point of which they seem to spring. In the absence of intermediate conditions, this California form would be specifically separated from the Eastern ones without question. It seems preferable, however, as in the case of *E. lactiflua*, of which they may prove to be the chlamydosporic condition, to include them under one name until we know more about them. It must be acknowledged, nevertheless, that the variations above enumerated may prove too great to justify this procedure, and it is possible that, as in the case of *E. lactiflua*, in the light of further information, more than one species may emerge from this rather too comprehensive assortment.

I am indebted to Miss Wakefield of the Kew Herbarium for an opportunity to examine a portion of the type of *E. australis* Berkeley, from Tasmania. The spores are like those of *E. macrocarpa*, the

maximum diameter observed being 170 μ . In all its characteristics it comes well within the variations of the present species, and there seems to be no reason for maintaining it as a distinct form.

Endogone pampalonia Baccarini (1903), p. 90, has been examined, through the courtesy of Professor Mattiolo, who has kindly communicated a slide of microtome sections from the type of this species. Like most sections of this nature, they are of little use for the purposes of specific determination, and it is difficult to decide from them what the distinctive characters, if such exist, really are. Baccarini based the species on the fact that the hyphae between the spores are more copiously developed and compactly woven than in the usual types of *E. macrocarpa*, in which he conceives the spores, "ampolla," to be simply gregarious, while in *E. pampalonia* they form a "cumulo," which he regards as a transitional condition between the loose heap formed in *E. macrocarpa*, and the more definite sporocarp of *E. lactiflua*. The different origin of the spores in *E. lactiflua* would, however, destroy any significance in such a series. The spores correspond in size to those of *E. macrocarpa*, 120–140 μ , but have much thinner walls, owing perhaps to the immature condition of the specimen. As has been mentioned above, similar conditions have been found in New England, although the compact "gleba" is characterized by the usual thick-walled spores, and the same is true of Californian material. Until we have much more information concerning the variations of *E. macrocarpa* it seems desirable to regard *E. pampalonia* as at best no more than a variety of this species.

Endogone tenebrosa nov. sp.

(Fig. 46.)

Spore-mass spongy, easily disintegrating, blackish. Hyphae loose and friable, 8–40 μ in diameter. Chlamydo-spores spherical or subspherical, 200–270 μ , the largest 260 \times 275 μ , brownish yellow, becoming quite opaque at maturity, the reddish brown wall becoming 15–20 μ thick and finally invisible; surrounded by a thin hyaline exospore.

In Sphagnum. Little Metis, P. Q. E. C. Jeffrey.

The material of this species is so broken up in the fluid in which it is preserved that it is difficult to determine what was the original form of the irregular spongy masses. The huge spores are readily visible with the naked eye, and become absolutely opaque from the darkening

of the contents, and finally of the thick endospore, which, at maturity, is invisible even with bright illumination, and is surrounded by a very thin hyaline exospore. Though sometimes slightly irregular, or slightly longer than broad, they are as a rule rather uniformly and evenly spherical. In structure and development they correspond to those of *E. macrocarpa*: but are even more closely comparable with those of the species referred to below, which was found in the stomach of a shrew.

ENDOGONE MICROCARPA Tul.

(Figs. 35-37.)

Tulasne (1851), p. 182, Plate XX, fig. 2. Bucholtz (1912), p. 192, figs. 75-76. nec Rabh. Fungi Europaei No. 2516.

Glomus microcarpus Tulasne (1845), p. 63.

This species has been recorded from America only on the authority of Harkness (1899), who collected what he regarded as this form in the forest at Mill Valley, California, No. 237. The description which he gives does not make at all clear what he had before him; but the corresponding number from the Harkness Collection, which has been kindly sent me for examination by the Stanford University Herbarium, proves to correspond to some of the forms of *E. lactiflua*, the spores being clearly zygospores.

A form, however, identical in all respects with the figures and description of Tulasne, has been kindly communicated to me by Dr. C. W. Dodge; who collected it in June, at Aldercroft Creek, Los Gatos, California. The spore-masses are well formed, though rather small, firm and similar to those of *E. macrocarpa* in form and color. The spores are nearly spherical, 40-48 μ , and very thick-walled.

Although there have been various records of this species in Europe, it does not appear, from published accounts, that it has been recognized with certainty since the original records of Tulasne, by whom it was found in Italy and France; and it seems to have been confused with smaller types of *E. macrocarpa*. Some of the latter from America serve in a measure to bridge the gap between the two species, but *E. microcarpa*, with a rather constant maximum spore diameter of 48 μ , seems clearly distinguished. The accounts of Tulasne and of Bucholtz, who reexamined the original types, should be consulted for further information in regard to this species.

Endogone radiata nov. sp.

(Figs. 47-51.)

Fruiting body variously lobed, whitish, becoming yellowish brown in alcohol, about 10×5 mm., the dried specimen about 5 mm. Gleba tough, dense, nearly homogeneous, the closely coherent rather slender elements hardly distinguishable, yellowish with a fibrous appearance; the peridial layer rather thin, darker brownish, the superficial hyphae usually producing terminal and intercalary vesicular enlargements with distinguishing septa. Spores scattered, sometimes rather distant, sometimes with a slight tendency to grouping, rarely spherical, usually with the longitudinal axis considerably greater than the transverse, oblong, elliptical or subpiriform, often irregular from pressure, the long axis more or less coincident with the radius of the fruiting body, 68×38 - 85×50 μ , borne terminally on often clearly recognizable simple hyphae, somewhat stouter than those which compose the substance of the gleba. The spore-wall shows no visible distinction between exospore and endospore and is from 4-5 μ thick: the contents rather finely granular, pale brownish yellow.

Under the leaf cover in spruce woods; Gerrish Island, Kittery Point, Maine; Intervale, N. H.; August, 1896 and 1901: in Sphagnum, Little Metis, P. Q. E. C. Jeffrey.

This species was first taken for *E. microcarpa*: but is certainly distinct. Its spores are rarely spherical although they appear to be so when cut transversely; the wall is comparatively thin, and is not visibly double. The radiate arrangement of the spores, which are firmly embedded in a dense fibrous matrix, seems to be characteristic; but is lost as soon as the section deviates from the radial direction. In the specimens from Kittery and Little Metis, the surface of the peridium shows numerous short projecting filaments with swollen terminations, and intercalary vesicular cells of no great size. At Kittery Point this species was found in company with *E. incrassata* which was supposed, at the time, to be the same. It is thus not now possible to say whether it had the same alliaceous odor. None was noticed in the Intervale material. Among the rather numerous individuals collected by Professor Jeffrey, there are no individuals of *E. incrassata*, as far as has been ascertained. Any connection between the two is thus problematical.

Endogone arenacea nov. sp.

(Figs. 38-40.)

Spores associated in an indefinite mass through which the material of the substratum (sand) is uniformly and copiously distributed, the whole bound together in an irregular crust-like aggregation, by a loose white mycelium of occasionally septate hyphae. Spores, chlamydospores, rather uniformly spherical, thick-walled, brownish yellow, about $70\ \mu$ in diameter ($65-75\ \mu$): the walls $5.5-6.5\ \mu$; with KOH, $8\ \mu$.

Near margin of brook, Maraval Valley, Port of Spain, Trinidad, B. W. I., in sand under trash.

This species was found at no great distance from the gathering of *E. fulva*, hereafter mentioned, from the same locality. The spore-mass has the appearance of a bit of caked sand, about 16×15 mm. and about 4 mm. thick when dry. The rather scanty mycelium is visible with a lens over the surface, but it would be unlikely to attract attention, and was preserved and examined almost by accident. The mass is less characteristic and more amorphous than that of any other species, unless it be *E. multiplex*. The spores, although they show occasional variations in outline and slight differences in size, are exceptionally uniform in these respects as compared with other chlamydosporic types, and are usually quite spherical. The very thick endospore is not continuous, and no septum is present: the thin, often hardly distinguishable, exospore is usually externally roughened by adherent more or less granular disorganized material. The hyphae are much bent and tangled between the spores and sand grains, and the spores often arise from a very short branch. Their non-sexual origin is, however, unquestionable. When treated with potash a rather characteristic smoky stain appears about their insertion, Figure 40. The fatty contents is apt to develop acicular fat crystals, Figures 38, 40. The hyphae show the usual irregularities seen in other species of the genus, and are very rarely septate.

Endogone canadensis nov. sp.

(Figs. 52-55.)

Sporocarp subspherical or irrègularly lobed; soft, but rather firmly coherent, with a rather well defined whitish (?) peridial layer: gleba dark brown. Spores distinguished by a septum, ovoid to ellipsoid, or

somewhat asymmetrical, $70-80 \times 54-58 \mu$ very rarely $100 \times 65 \mu$; the wall hyaline or pale yellowish, 4μ thick. Hyphae $8-14 \mu$, of the usual type, with occasional clearly defined septa; the sporophores characteristically slender, $5-6 \mu$.

In Sphagnum, Little Metis, P. Q. E. C. Jeffrey.

The spore-mass in the material examined, which is all alcoholic, is similar to that of *E. radiata*. The gleba, however, does not consist of a firm dense matrix in which the spores are firmly held, but is formed of a loose mesh of friable mycelium, of the usual type, in which the spores are free, and are associated with numerous vesicular mostly spherical abortive spores of variable size which eventually shrivel and turn brownish.

The species is most nearly related to *E. fulva*, but is distinguished by its decidedly smaller and more regularly ovoid spores, which are borne on characteristically slender sporophores, and separated by a septum. The nearly hyaline wall of the spore is relatively distinctly thicker; the exospore thin, but rather clearly defined. The fatty coarsely granular contents is at first hyaline, becoming brownish.

Endogone borealis nov. sp.

(Figs. 44-45.)

Spore-mass irregular, coherent, spongy, dark, almost chocolate brown, about seven to eight mm. in greatest diameter. Gleba of loosely woven hyphae, $10-25 \mu$ in diameter, among which much foreign matter and many abortive spores are incorporated. Spores reddish brown, broadly and rather symmetrically elliptical, about $125 \times 100 \mu$, the larger $145 \times 110 \mu$: the thick red-brown walls about 8μ : borne on rather slender hyphae and frequently subtended by a septum.

In Sphagnum, Little Metis, P. Q. E. C. Jeffrey.

This species seems clearly distinguished by the form and color of its thick-walled spores, the contents of which, in the alcoholic material examined, forms a rather finely granular more or less fibrous protoplasmic network. It does not seem nearly related to other known species unless it be *E. canadensis*, from which it is distinguished by the peculiar color and broadly and symmetrically elliptical outline of its large thick-walled spores. The endospore is not continuous when examined under brilliant illumination although the isthmus is a very narrow one and a small septum appears to be present.

ENDOGONE PULVINATA Henn.

(Figs. 41-43.)

Hennings (1897), p. 212: nec Lloyd (1918), p. 800, fig. 1240.

Dr. Lindau has very kindly allowed me to see a fragment of the type of this species, collected by Gollmer, and found growing on the ground at Caracas, Venezuela. The specimen, which is not in the best condition, resembles *E. fulva* in general appearance and color. The spores, however, although they have thin walls like *E. fulva* and are similarly separated from the hypha by a septum, are distinctly different in general appearance, being more nearly spherical, often asymmetrical, and seldom showing the considerable difference between the two diameters that is so characteristic in the last mentioned species. The larger spores are $85 \times 85 \mu$ or $75 \times 85 \mu$, according as the axes tend to vary slightly: the average being about $75 \times 75 \mu$ or $75 \times 70 \mu$, with considerable variation below these dimensions, and no little variation in outline. The walls are $2-4 \mu$ thick, as in *E. fulva*, and the hyphae which, in the specimen seen, are for the most part disorganized, appear to be entirely similar and loosely woven.

ENDOGONE FULVA (Berk.) Pat.

(Figs. 56-59.)

Paurocotylis fulva Berkeley (1873), p. 137.*Endogone Moelleri* Hennings (1897), p. 211.*Endogone lignicola* Patouillard (1902), p. 183. Bucholtz (1912), p. 199, figs. 97-99.*Endogone fulva* Patouillard (1903), p. 341; Bucholtz (1912), p. 200, figs. 97-99.*Endogone pulvinata* Lloyd (1918), p. 800, fig. 1240, nec *E. pulvinata* Henn., (1897), p. 212.

Patouillard first called attention to the fact that *Paurocotylis fulva* belonged to the genus *Endogone* and that it was unrelated to *P. pila* Berk. which is the type of the genus. From the data and figures given by Bucholtz, who has examined the original material in both instances, the identity which he suggests between *E. fulva* and *E. lignicola* seems almost certain. The fact that they occur in widely separated regions, the one in Ceylon, the other in the West Indies, is shown to be of little significance; since other species, like *E. malleola* may have, as will be seen, an equally wide distribution.

I have collected this species in abundance in the Maraval Valley near Port of Spain, Trinidad, growing subgregariously along the Maraval brook in moist bamboo trash, fruiting within this material and running out to produce its fructifications on the surrounding sand and pebbles. A single specimen was also found under the leaf cover in the forest about the Grand Etang, Grenada; and I obtained several typical specimens growing exposed on rotten logs in Boggs' Hammock, a short distance south of Cocoanut Grove, Florida.

Dr. Lindau has been so kind as to send me a fragment of the type of *E. Moelleri*, described by Hennings from Brazil. This material is, as above indicated, identical with the Trinidad form, which has been submitted to M. Patouillard and is pronounced by him in all respects the same as his *E. lignicola*. The spores of the Brazilian form have the darker color which seems to be more characteristic of individuals which have developed in humus, without exposure to the light and air, and are, as in the Grenada gathering, sometimes almost opaque when first mounted.

Mr. Lloyd has also been so kind as to send me a portion of the Jamaica material figured by him (l. c.) as *E. pulvinata* Hennings, as well as a second specimen collected by Mr. Brace in the Bahamas. These gatherings also correspond in all respects to the Trinidad form, and must be regarded as typical *E. fulva*. I have further received from Professor Mattirollo for examination, a specimen collected by Rick in Brazil, which also has all the essential characters of the present species, although the spores are not turgescens: and from Professor Spegazzini a gathering from La Boca, Buenos Aires, doubtfully determined as *A. argentina*, which seems quite typical of this species, although not in very good condition.

The spore-masses of *E. fulva* vary from $1\frac{1}{2}$ cm. to a few mm. in diameter when dry, and are usually umbilicate below, subspherical to flattened and irregularly lobed; and even in the same gathering there may be great variation in color. The peridium, which is usually well developed, although in some specimens it may be absent to a greater or less extent, exposing the naked spore-mass, is at first pure white and floccose in young fresh individuals, turning brownish with age, or when handled, the color deepening from ochraceous tawny to chestnut brown.

The hyphae are of the usual type, rather stout, 8-12 μ in diameter, more or less, often nodulose or irregular, showing occasional septa, which are more frequent than in most other species, and are in some cases quite loosely interwoven.

The spores vary considerably in color, even in the same individual; and although sometimes nearly opaque, "atro olivaceis vel atris," may, when produced free to the light and air, have a decidedly pale, yellowish color. Their outline is characteristically oblong, elliptical to oval or even subpiriform, rarely nearly circular in outline, except when viewed end on. They may be more than twice as long as broad, e.g. $125 \times 55 \mu$, and ordinarily show a decided difference between the long and short diameter; the average variation being from $50-125 \times 45-70 \mu$. The wall, although thin as compared with some forms of *E. macrocarpa*, for example, is thick, $2-4 \mu$, in contrast to the walls of the sporangial types. Bucholtz makes a separate category, a fourth subdivision of the genus, to include this somewhat thinner walled type of spore, and speaks of them as possible sporangia. Having examined a large series of specimens in all stages of development, and from widely separated localities, it seems evident that they are certainly nothing more than chlamydospores, having somewhat thinner walls than those of the more familiar species, and being distinguished by a septum. The attachment of the spore is often sublateral, as is indicated in figure 97 of Bucholtz, and the sporogenous hypha is often, though by no means invariably, somewhat narrower just below the point of attachment.

The contents of the spores may be rather dense and uniformly granular, or is often somewhat stringy in appearance apparently from the presence of fatty crystalline structures. The species is most nearly related to *E. pulvinata* and the other forms in which the spore is distinguished by a basal septum.

ENDOGONE RENIFORMIS Bres.

(Figs. 60-71.)

Bresadola (1896), p. 297.

Endogone ? argentina Spegazzini (1899), p. 300.

Through the kindness of Professors Lindau and Spegazzini I have been able to examine the type material of *E. reniformis* Bres. collected by Möller in Brazil and of *E. argentina* collected at Santa Catalina, Llavallol, Argentina. The Abbé Bresadola has also sent me a third specimen collected by Rick in Brazil, and I myself found apparently the same form in the antarctic forest at Punta Arenas, Magellanes, Chile.

A comparison of these four gatherings indicates that, although the spores of the Magellan specimen are distinctly larger, the other three are not separable, and correspond in all essentials. Bresadola, in his description, speaks of monosporic asci in which the spore is clearly distinguished, but was probably misled by the appearance of young sporangia in which the contents was still continuous, not having yet divided into spores.

The sporangiocarps of this species which occur on or just under the leaf cover, are subspherical to reniform, umbilicate, yellowish when dry, nearly white when fresh, 4-10 mm. in diameter, sometimes 20 mm. according to Spegazzini, and arise from a rosy mycelium which may form a more or less distinct stalk as in *E. malleola*. In the specimens examined there is no peridial layer distinguishable, the surface being composed of sporangia and slightly projecting scanty hyphal elements. The fertile hyphae are sparingly septate and branched, bearing the sporangia terminally and diverging from a cushion-like basal region associated with the umbilicus. The sporangia are more commonly spherical, but, as in *E. malleola* may show variations in length and breadth and may be asymmetrical in outline (Figs. 61-62). At maturity the sporangium wall collapses about the spores and follows their irregular contour. The average diameter is about 35-40 μ , but may reach 60 μ or over. The spores, which are evidently formed by cleavage of the whole contents in these sporangia, vary in number from four to a dozen or even more, although Spegazzini mentions eight, only, and are rather variable in size and irregular in shape from mutual pressure. In the Brazilian and Argentine material, Figures 64-71, they are 12-30 \times 12-25 μ the average about 18 \times 20 μ , but in the Magellan material, Figures 60-63, they are for the most part distinctly larger, 20-38 \times 14-34 μ . The number present in a single sporangium varies from four to a dozen or more; although, as stated by Spegazzini, there are often not more than eight. This number is, however, by no means constant or even characteristic. On the rupture of the sporangium wall they are readily set free, although when fully mature, Figures 67-68, they appear to be held by the collapsed sporangial wall and rather firmly coherent. They are quite hyaline and contain, as a rule, one or more large oil globules or coarse dense granules.

A second Argentine collection from La Plata sent me by Spegazzini doubtfully determined as this species, proves to be *E. fulva*, as already mentioned.

ENDOGONE MALLEOLA Harkn.

(Figs. 72-78.)

Harkness (1899), p. 280, Plate XLIV, figs. 22 a & b.

Endogone microcarpa Fischer pro parte (1897), p. 121, figs. 4-5. Rahenhorst Fungi Europei, No. 2516, nec Tulasne (1851).*Endogone pisiformis* Bucholtz (1912), p. 196, figs. 88-96; nec Link (1809).*E. Torrendii* Bresadola. In Torrend (1913), p. 101: (1920), p. 55. Torrend (1913), Fungi Selecti Exsiccati, No. 159.

This species seems to have been responsible for much of the confusion with which the genus has been afflicted, since, although it is fundamentally unlike the majority of the other types which have been included in *Endogone*, it bears certain resemblances to them which have led to a misconstruction of appearances that are frequently found in the spores of the other two sections of the genus. This misconception has led to the opinion that the chlamydo-spores, for example, were to be regarded as sporangia, or at least that they might become directly transformed into sporangia. This conclusion, however, seems to have no better basis than the fact that, in many cases, the contents of these spores is so modified, that they become filled with large granules or fatty bodies, often so uniform in size and form that their spore-like character has been assumed. Thus Bucholtz in his *Beitrag*, influenced probably by the use of the terms sporangium and sporangiolium in Link's description, has assumed that the present form may be regarded as the true *E. pisiformis*, and is thus the type of the genus. The reasons for believing that this reference can hardly be correct, have already been mentioned. In *E. malleola*, however, the large spherical or somewhat irregular bodies which form the fructifying mass are filled with numerous relatively large, separable, walled spores; quite different in appearance from any differentiation such as has been above referred to.

The references to this species which occur in the literature, are for the most part based on the material collected by Vittadini in the vicinity of Naples and distributed in the Fungi Europaei under *E. microcarpa*. Fischer (1896) assuming that the determination was correct, and that the material showed a condition of this species in which the chlamydo-spores had become transformed into sporangia, regarded it as a demonstration of the sporangial or hemiascoid nature of the spores of *Endogone* in general.

The significance of this condition has been variously discussed, and the terms ascus and sporangium variously applied to it. Its resemblance to the sporangium of the Mortierelleae was first pointed out by Baccarini (1903), who believed that it should be excluded from the Endogoneae for this reason. The researches of Bucholtz who demonstrated the sexual origin of the spores in certain species, and the necessity of their inclusion among the Mucorales, gave further support to this suggestion of Baccarini, and, assuming that the three sections herewith distinguished actually represent conditions of a single generic type, the view that the members of the family are close relatives, at least, of the Mortierelleae, is, as has been already pointed out, strongly supported by the fact that in this family alone among the Mucorales, does one find zygosporangia having specialized envelopes, associated with highly developed acrogenous chlamydospores; and sporangia separated from the sporangiophore by a simple septum. It should be remembered, however, that although the two may be provisionally thus associated, the apparent parallelism is not necessarily more than a coincidence.

The second record of this species is that of Harkness (1899) who first described it under the name *E. malleola* from material, collected on Mt. Tamalpais in California, which I have had the privilege of examining, and which differs in no essential from the Naples material, although the maximum diameters of the latter are often greater (Figs. 72-74).

The form was not again reported till specimens collected in Portugal were described as *E. Torrendii* Bresadola, Figures 75-76, in an enumeration by Torrend (1913) of the second century of his *Fungi Selecti Exsiccati*, published in Brotéria. Quite recently this description has been republished by Bresadola (1920) among his *Selecta Mycologica*, where, however, the fact of its distribution by Torrend is not mentioned.

Its range has been further extended by its discovery in New Zealand where material, having dimensions somewhat greater than those of the Naples gathering, has been collected by Mr. James Mitchell, and very kindly communicated to me by Mr. Lloyd (Figs. 77-78).

If one compares these different gatherings, although there is a general agreement in the form, structure and color of the fruiting masses, which are very similar to those of *E. argentina*, the average size of the sporangia and the number of spores which they contain is subject to considerable variation. Treatment with potash, slight pressure of the coverglass, and degrees of maturity, have to be considered in such a comparison; but quite apart from these, there is a

marked difference observable even between individuals of the same gathering. Thus of two individuals from the Torrend distribution, one shows sporangia with an average diameter of 55–60 μ , while those of the other average from 70–75 μ or slightly over, the latter dimensions corresponding to the Californian and Naples gatherings. Although Bucholtz reports a maximum diameter of 116 μ for the latter, I have not seen any above 100 μ in the specimen examined. The New Zealand form, on the other hand, is distinctly larger, the maximum diameter being 120 μ , diameters of 100 μ being common and the average being 80–85 μ .

The form of the sporangium is normally subspherical, but may be irregular, longer than broad, or even broader than long, or subangular from mutual pressure. The wall usually appears thin, and tends to follow the contour of the contained spores; but, especially when treated with potash, may form a clear gelatinous envelope around the spores, 4–5 μ thick. The spores are somewhat variable in size, subangular from pressure, but often become spherical when free, and possess a distinct thin wall. None have been seen, even in the Torrend material, which closely approach the measurements given by Bresadola, 15–28 \times 15–17 μ . Measured in the sporangium they rarely seem to exceed 14–15 μ , and usually average from 8–12 μ : although when set free and treated with potash they may reach 20 μ occasionally. They form a rather viscous mass, and when the sporangium is violently broken, are apt to escape in more or less coherent groups. The filaments, on which the sporangia are borne terminally, are branched and usually rather copiously septate, even submoniliform; the contents above the upper septum, which is often a short distance below the sporangium, being often divided into several superposed spores.

From its general characters this form could probably be cultivated with ease by anyone who was fortunate enough to find it in a fresh condition, and a thorough examination of its development in pure cultures is very much to be desired.

DOUBTFUL OR EXCLUDED SPECIES OF ENDOGONE.

Reference has been made above to the occurrence of spores of *Endogone* in the digestive tract of animals, and in this connection it may be mentioned that in one of these instances spores and mycelium were found in the stomach of a shrew, sent me by Mr. Judd from the vicinity of Washington, D.C. In this material, scanty but typical *Endogone* filaments bear a few very large spores, some of them 240 μ

in diameter, similar to those of *E. macrocarpa*, when young, but becoming quite opaque as they mature, owing to a blackening of the exospore. This cannot apparently be referred to any of the described species, although it is very similar to *E. tenebrosa*. The opacity of the spore, however, seems due rather to the formation of a black encrustation than to a gradual darkening of the contents such as takes place in *E. tenebrosa*.

A second type found in the digestive tract of a myriopod collected in Eastern Tennessee, appears also to belong to an undescribed Endogone. The hyphae and spores are typical of this genus, the latter brownish yellow, mostly longer than broad, the greater diameter about 38–45 μ , the walls not greatly thickened, peculiar from its slightly one-sided insertion on the sporiferous hyphae. Its size is very near that of *E. microcarpa*, but it differs in its much thinner wall, asymmetrical insertion and more elongate outline. On the other hand it differs from *E. fulva* in its smaller spores with relatively thicker walls.

A third form, which approaches more nearly to some of the variations of *E. macrocarpa*, was observed by Dr. Weston while working with water moulds in the Harvard Laboratory. It produced a rather scanty growth, consisting of a single subdichotomously branching hypha having all the characteristics of those peculiar to the genus. This grew in water about a fly, attacked by Saprolegniae, and produced abundant spores rather thin-walled, subspherical, pale brownish yellow, the larger 85–100 μ in diameter. It is quite probable that this represents a form of *E. macrocarpa*, modified by its growth under unnatural conditions.

E. Tozziana Sacc. & Cav. has been referred to *Leucogaster*, a disposition which is confirmed by an examination of a portion of the type.

SPHAEROCREAS Sacc. & Ell.

Type species

SPHAEROCREAS PUBESCENS Sacc. & Ellis.

(Figs. 79–82.)

Saccardo & Ellis (1882), p. 582.

Stigmatella pubescens Saccardo (1886), p. 680.

Sclerocystis pubescens von Höhnelt (1910), p. 399.

This species was based on rather scanty material collected on leaves and sticks at Newfield, New Jersey, by Ellis; a portion of which has

been examined in the Farlow Herbarium. For some inexplicable reason it was later associated in the fourth volume of the Sylloge, in the genus *Stigmatella*, with a second form, *Stigmatella aurantiaca* B. & C., a wholly different organism belonging to the Myxobacteriaceae, as I have formerly pointed out (Thaxter (1892), p. 402), where the close relationship of *S. pubescens* to *Endogone* is also referred to. Von Höhnelt (1909), p. 127, includes in this genus his own *S. javanicum*, as well as the two species included in *Ackermannia* by Patouillard; although in a later paper (1910), p. 399, he transfers all of these to *Sclerocystis* B. & Br., reducing his own species, *S. javanicum*, to a synonym of *S. coremioides* B. & Br. Although this disposition seems correct, in so far as the others are concerned, it is certainly not justified in the case of the present species which has no characters which would indicate a near relationship to *Sclerocystis*.

Sphaerocreas pubescens is by no means an uncommon fungus, and is probably widely distributed. It has been repeatedly collected in moist woods and maple swamps at Kittery Point, Maine, and its vicinity, and has been also found at Intervale, N.H. by myself and at Chocorua by Dr. Farlow. It usually produces its fructification on dead leaves or twigs on the leaf cover, or on rotting branches, and in one instance was found in some quantity about old carrion. Less often it has been found on Sphagnum, like *E. pisiformis*, which it resembles very closely in general appearance; although it is usually much smaller, .2-2 mm., subgregarious, and paler in color when fresh, with a much more conspicuous external tomentum. The resemblance is so close, however, that Krieger appears to have included specimens of both in the miscellaneous gatherings which he has distributed in the *Fungi Saxonici* under *Endogone pisiformis*, No. 1651. In the Harvard copy at least, one of the two individuals examined proved to be *S. pubescens*, which, as far as I am informed, is the first European record of its occurrence; while the other was typical *E. pisiformis*, as I have interpreted it. It is at once distinguishable, however, from the small size of the subspherical, or broadly elliptical spores, Figures 81-82, which are $18 \times 15-25 \times 22 \mu$, rarely larger, although Saccardo mentions a maximum of 30μ . The spore-walls are relatively thick, $1.5-2.5 \mu$, and distinctly yellowish, while the contents appears to be hyaline or nearly so; usually with one or more large oil globules, associated with a variable number of small granules, but seldom uniformly and densely granular. They are produced acrogenously on very fine branching thick walled, refractive hyphae, 2μ or less in diameter, with few if any visible septa, and are distributed indis-

criminated throughout the compact mass, which becomes very hard on drying. On the surface of the spore-mass, which is subspherical, slightly umbilicate, and rather firmly attached to the substratum which it may partly envelope (Fig. 79), the hyphae gather in rather regularly disposed, compact, attenuated, radiate, discrete bundles, Figure 80, 60–100 μ in length and 12–30 μ at the base, while the apex may be less than 2 μ . The hyphal elements which form these bundles are so firmly and closely coherent that the individual filaments which compose them can only be distinguished with a high magnification or by crushing them apart. They form the conspicuous superficial tomentum which, although it may be less evident in older specimens, is very striking in younger individuals (Fig. 79).

Although the peculiarities of the hyphae and spores above referred to, might not be regarded as very convincing evidence for the separation of this species from *Endogone*, I have preferred to keep it distinct provisionally. The indiscriminate distribution of its spores in a solid mass would certainly forbid its inclusion in *Sclerocystis*, as represented by *S. coremioides* and *S. Dussii*, in both of which they are disposed "en une seule zone radiale," about a central columella.

The rather close resemblance between the general appearance of this species and that of *Endogone pisiformis*, above alluded to, might suggest that they were possibly stages in the cycle of a single fungus; *S. pubescens* representing the chlamydosporic condition of the zygosporic type. The character of the hyphae appears to be so different in the two cases, however, that such a connection seems very improbable, and although their habitats are similar, I have never seen them closely associated in Nature.

SCLEROCYSTIS B. & Br.

Berkeley & Broome (1873), p. 137.

Xenomyces, Cesati (1879), p. 26.

Ackermannia, Patouillard, (1902), p. 180.

Type Species

SCLEROCYSTIS COREMIOIDES B. & Br.

Berkeley & Broome (1873), p. 137, Plate X, fig. 56.

Xenomyces ochraceus Cesati (1879), p. 26.

Sphaeroceas Javanicum von Höhnelt (1908), p. 30, fig. 1.

Von Höhnelt, who examined the original types, vouches for the identity of his *Sphaeroceas Javanicum* and of *Xenomyces ochraceus* Ces., with *Sclerocystis coremioides* B. & Br., and an examination of the type material of *Ackermannia* which M. Patouillard has very kindly communicated seems to bear out his conclusion that this genus must also be regarded as a synonym. It appears to belong in the Endogoneae, the characters of its spores and hyphae being in general similar to those of Endogone. The three species seem to conform to a well marked generic type, and are distinguished from Endogone in producing numerous small sclerotium-like sporocarps in which a well defined sporogenous layer is very characteristic, the large spores lying side by side with their long axes directed radially from a central columella-like region.

Von Höhnelt states that the sporocarps in his material, which was found in the Buitenzorg garden growing on bits of wood and sticks, were "zu einer festen porösen Maase verwachsen." They are represented as short-stalked, 500-600 μ broad, hard, dull yellow to grey-green, sometimes becoming superposed through distal proliferation. The closely woven hyphae are said to be septate, those of the short stalk 8 μ in diameter, those which occupy the central portion of the sporocarp about 4 μ , as are those which form a well defined outer layer; their free terminations showing no indication of special or characteristic modification. The spores as represented are placed side by side, as already described, immediately beneath this outer layer, and are long oval to long elliptical or even clavate, 60-90 \times 20-50 μ . Their walls appear to be thin, and the contents is either finely granular or wholly lacking.

The type material of Berkeley and Broome in the Kew Herbarium was found in Ceylon and was regarded by Petch (1908) p. 116, as a sclerotium. Later, however, (1912) p. 282, he confirms the statement of von Höhnelt as to its identity. The type of Cesati, now in the Herbarium of the Royal Gardens at Rome, was collected by Beccari in Borneo.

SCLEROCYSTIS DUSSII (Pat.) von H.

(Figs. 83-85.)

von Höhnelt (1910), p. 390.

Ackermannia Dussii Patouillard (1902), p. 181, figs. a-g.

Sphaeroceas Dussii von Höhnelt (1909), p. 401.

This species, which was collected by Ackermann in Martinique and by Duss near Basse-Terre, corresponds very closely in general charac-

ters to the preceding species. It is said to form a superficial, golden yellow, more or less reddish "stroma," forming a crust or cushion, and covered with yellow giant cells $260-400 \times 50-100 \mu$. The individual stromata are rounded or ovoid, solitary and scattered, or contiguous and confluent; each containing a "perithecium" (sporocarp), or two to three superposed, about one third of a millimeter in diameter, completely surrounded (entourés) by the stroma. The spores, (thèques) are rounded ovoid, brownish yellow, $70-130 \times 35-100 \mu$, the walls thick; the sporogenous filaments $12-16 \mu$ in diameter: they form a single radial zone lying side by side in a single layer with the long axis radially directed. The sporocarps ("perithecia") are hard and sclerotium-like, whitish, formed from interwoven hyphae which are thick-walled, colorless and $4-5 \mu$ in diameter, surrounding the sporogenous layer, those on the surface terminating in characteristically modified broadly fusiform swollen extremities, or by a series of two or three such enlargements.

M. Patouillard has been so obliging as to send me two fragments of the type, one of which is comparatively young. From an examination of these specimens it would appear that the fungus arises in yellowish patches which may become variously confluent. This mycelial layer, crust or stroma, is made up of two distinct elements: relatively slender and thick-walled, branching, interlaced, aseptate hyphae extending radially and giving rise to the sporocarps: and large septate hyphae, the swollen segments of which are thin-walled and usually closely coherent, forming the covering of giant cells mentioned by Patouillard, as well as a rather scantily developed lysigenous matrix about the sporocarps, which appear to become completely free through its ultimate disappearance. On the surface of the crust or stroma, these cells, which appear very irregular in outline, though radially elongate, form a yellow pseudotissue, Figures S3-S4; the whole at first continuous, but later, and on drying, becoming cracked and broken into irregular areas, with uneven elevations of the surface which correspond in a general way to the sporocarps lying immediately below them. Beneath this crust, the sporocarps are crowded, at maturity, in a loose dry mass, and may be supposed to be scattered separately when freed by its disintegration.

The younger specimen examined shows the sporocarp-origins still in process of formation immediately beneath the surface of the crust, as well as the more or less clearly defined relation of superposition which the older sporocarps continue for a time to bear to one another. Their temporary coherence is due to connecting wefts of smaller, relatively

thick-walled, slender, intricately interwoven aseptate hyphae above mentioned, which form the second element of the mycelial crust, or stroma. How these wefts at first originate, it is not possible to determine from the material; but as they develop, a distal portion is distinguished from a basal, which forms a very short stout stalk, usually broader than long, but variably developed in different cases; and the broadening distal portion organizes the sporocarp proper. In this process the latter becomes differentiated into a central region, or columella, continuous with the stalk, and surrounded by a sporogenous layer from which the long oval to somewhat wedge-shaped or subclavate thick-walled brownish yellow spores diverge radially; lying side by side in a single layer which completely surrounds the columella, except in the basal region, where it remains continuous with the stalk (Fig. 83). A section of the sporocarp in this condition suggests a mushroom "button" in general outline.

The sporogenous layer, which occupies the surface of the columella, is thin and somewhat more dense. The spores, which radiate from it with great regularity, are rather uniform, with somewhat flattened extremities, and are attached by a pointed base, which is usually distinguished by a small well defined septum from its origin in the sporogenous layer (Fig. 85). Owing to the confused structure of the branching, densely woven elements which form the sporogenous layer, it has not been possible to determine the exact nature of these origins. Even in thin sections, I have been unable to determine satisfactorily such a simple and continuous relation, between the spores and the hyphae of the columella, as is shown by the figure of Patouillard in this species; or in that of *S. coremioides* drawn by Weese, in von Höhnel's *Fragmenta*, No. 174, fig. 1; which appears to be somewhat diagrammatic. Although it is not impossible that some form of conjugation may occur in this layer, which is hidden by the confusion of cut ends, loops and convoluted branches, I have seen nothing in the dried material that could be thus interpreted. The thin-walled spores with their basal septum suggest a resemblance to the corresponding type in *Endogone* illustrated by *E. fulva*. It may be said in this connection that the extraordinary definiteness of the spore-relations is not such as one would expect in a chlamydosporie type; but might possibly be interpreted as a higher development of the tendency to segregate somewhat specialized spore-groups, which has been above described in certain sexual species of *Endogone*, like *E. multiplex* or *E. tuberculosa*, and in the chlamydospores of *E. vesiculifera* and *E. fasciculata*.

The intersporal spaces are traversed by hyphae which grow radially from the columella and form, outside the spores, a layer about $40\ \mu$ thick of intricately woven filaments, which are also continuous externally with the similar hyphae of the stalk. After a given sporocarp has developed, this outer layer proceeds to organize one or more new wefts of hyphae, which may be terminal or sublateral or both, and these wefts in turn organize new sporocarps in a manner similar to that which has been just described (Fig. 84). The successively formed sporocarps may thus be arranged in series corresponding to the successive origins of these wefts; either in simple rows, or in a more complicated fashion, owing to divergence from the long or radial axis.

The stalk-portion which is often but slightly developed, shrivels and separates from its point of origin, as the maturing sporocarp becomes hard and sclerotic, and persists as an inconspicuous tuft of shriveled filaments; the lysigenous elements above referred to having also disappeared and freed the sporocarps from their lateral attachments.

After examining a number of sporocarps with some care, I have been unable to detect either in young or in more mature conditions the peculiar subfusiform superficial hyphal terminations figured and described by Patouillard, as above indicated. When fully mature and freed from its attachments, the hard sclerotic sporocarp is externally furfureous from the numerous broken projecting ends of the filaments which cover it. Were the peculiarly swollen terminations seen by Patouillard normally recognizable, their presence should readily separate this species from *S. coremioides*, but since it seems certain that they are not always present, it is possible that the two species are not specifically distinct, even though the presence of the large celled evanescent pseudotissue is not mentioned in descriptions of the East Indian form. The spore-measurements, as given by von Höhnelt, are somewhat smaller, $60-90 \times 20-50\ \mu$; the average dimensions in the West Indian form, as I have determined them, being $95-115 \times 20-50\ \mu$; the extremes $60-120 \times 34-55\ \mu$, the shorter diameter being that of the distal end of the spore. The sporocarp measurements, on the other hand, as given for *S. coremioides*, are $500-600\ \mu$, while those of *S. Dussii* which I have measured are $350-450 \times 300-460\ \mu$. Although the spores of the East Indian form are thus somewhat smaller and the sporocarps somewhat larger than in the West Indian species, the discrepancy does not appear to be very great, as compared with other instances of variation in the group.

SCLEROCYSTIS COCCOGENA (Pat.) von H.

(Figs. 86-87.)

von Höhnelt (1910), p. 390.

Ackermannia coccogena Patouillard (1902), p. 183, figs. h-j.*Sphaerocreas coccogena* von Höhnelt (1909), p. 401.

I am indebted to M. Patouillard for a very small fragment of this species, which was collected by Ackermann in company with *Endogone lignicola* Pat., growing on rotten wood, the locality being the Plateau des Rivières, Martinique, and the date of collection June, 1901. This fragment shows a small portion of the crust or covering which surrounds the sporocarps, and three or four of the latter, which are fully mature, but still attached to it.

Judging from the original figures and description, the "stroma" of this species is more definitely circumscribed and thicker (6-8 mm. by 4 mm. thick) than that of *S. Dussii*, resembling closely the spore-mass of some *Endogone*, and covered by a more even and clearly differentiated pseudoperidial layer. The small fragment of this layer which I have examined, is composed of rather loose coarse septate hyphae, the segments of which are irregular and do not form a coherent pseudotissue of giant cells as in the preceding species.

The sporocarps are similar in form and appearance to those of *S. Dussii*, but somewhat larger, 400-675 μ in greatest diameter. The spores, which are similar in their origin and arrangement, are somewhat smaller, their average dimensions being about $100 \times 40-50 \mu$. The sporocarps themselves are at once distinguished, however, by the presence of numerous small spherical chlamydo-spores, Figure 87, similar to those of *Endogone*, which are formed terminally in the tomentum which covers the intricately woven superficial layer (Fig. 86).

In its thicker and more clearly circumscribed stroma, and more definite pseudoperidium, in its larger sporocarps and the production on their surface of spherical chlamydo-spores, and in the apparent absence of a lysigenous pseudotissue of large thin-walled hyphal segments, this species seems to be clearly distinguished.

GLAZIELLA Berk.

Berkeley (1879-80), p. 31, No. 8526.

Endogonella von Höhnel (1913), p. 294.

Type Species

GLAZIELLA VESICULOSA Berk.

(Figs. 88-94.)

Berkeley (1879-80), p. 31.

Xylaria aurantiaca Berkeley & Curtis (1868), p. 382, d.*Glaziella aurantiaca* Cooke (1883), p. 83; Lloyd (1919), p. 30, fig. 1460.*Hypomyces alboluteus* Ellis & Everhart (1893), p. 262 and 285.*Endogonella borneensis* von Höhnel (1913), p. 41, figs. 4-5.

Owing to its large size and conspicuous orange yellow color, this species has been repeatedly observed in the American tropics, but the early misinterpretation of its characters has led to much confusion as to its probable position. It was first collected in Brazil by Glaziou, No. 8526, this type, of which through the courtesy of Miss Wakefield I have been able to examine a portion, being still in the Kew Herbarium. Later, material collected by Wright in Cuba, a portion of which has been examined in the Curtis Herbarium at Harvard, was redescribed as *Xylaria aurantiaca* by Berkeley and Curtis, it being assumed in both instances that it was an immature ascomycete, and that its peculiarly developed spores were young perithecia. In a similar fashion a gathering from Jamaica, communicated by Cockerell was subsequently described by Ellis as a new but sterile *Hypomyces*, which he named *H. alboluteus* E. & E. Still more recently it has again been described under a new generic name by von Höhnel, as *Endogonella borneensis* n. g. et n. sp., this being the first record of its occurrence in the Eastern Hemisphere.

This plant occurs in the form of a bladder-like, variably lobed, or even convolute, soon unattached sporocarp, Figure 88, 2 to 4 cm. long by 2 to 3 cm. broad and 1.5 to 3 cm. thick, more or less, when dry; much larger when fresh. The tough gelatinous wall 700-900 μ thick, is perforate below, the perforation entering a central cavity which is quite empty. On drying it becomes hard and brittle and loses much of its color, fading and becoming brownish with age, and exposure. The outer surface is more even, with a slight bloom, the inner pale yellowish and somewhat uneven. A section of the wall cut

radially, Figures 89-90, shows a rather clearly defined distinction between an outer thicker, and an inner thinner dense layer and a looser broader sporogenous region which lies between them, but is not separated by any clean cut line of demarkation.

Although the fungus is usually described as immature or sterile, I have myself seen no specimens which are not fertile and but two that were even moderately young. Of these the youngest was found in 1891, near Kingston, Jamaica, partly buried in a very soft rotten log. The sporocarp was completely enveloped by a thin white separable universal membrane within which it was already free and perforate below. The hyphae composing this membrane are slender, thick-walled and septate. In this unexpanded condition, which was thick and somewhat flattened, the spores, although for the most part nearly mature, Figure 90, were crowded in an irregularly double layer, and the plant was set aside as a species of *Endogone*.

As the sporocarp matures and enlarges this crowded condition disappears, and the outer and inner layers, especially, evidently take an important part in the tangential increase, so that the crowded spores become more and more discrete as the wall stretches itself, so to speak, and eventually assume a more or less definite arrangement in a single layer. The hyphal elements which take part in this process are thick-walled with rather frequent septa, densely compacted in the two walls and somewhat looser in the middle region (Fig. 94). As the sporocarp increases in size the septa become very numerous and the filaments greatly enlarged, so that the inner and especially the outer layers appear to be made up of dense thin-walled parenchyma which gradually passes into the looser lacunose middle region, the hyphae of which are also thin-walled for the most part and submoniliform, Figure 93, with large interhyphal spaces.

Unfortunately no information is available as to the earlier stages in the formation of the sporocarp, or the initial processes of spore-formation. The sporogenous zone is evidently traversed at intervals by radial wefts of finer, closely septate hyphae, which are dense and have a dark granular appearance (Figs. 90-91). These wefts are the sporogenous centres above referred to, and conceal the spore-origins which traverse them. The spore-initials emerge from them as shown in Figure 91, a tangential section, in the form of long clavate structures, terminating apparently aseptate filaments which, although it has not been possible to trace them to their origin, appear to grow radially from the inner margin of the inner dense layer of the sporocarp. The tips of these clavate structures become greatly enlarged and the walls

enormously thickened; the lumen being sometimes almost obliterated. These swollen terminations push out into the interhyphal spaces of the middle zone, curving outward or backward, and are transformed to the mature spores. Sporulation seems to be more or less simultaneous at a rather early stage of development, and the enlargement of the orange sporocarp, after this has taken place, seems, under favorable conditions, to be a relatively rapid process.

The mature spores are very large, 200×200 – $415 \times 380 \mu$, spherical to broadly ellipsoid, a thinner gelatinous exospore about 10μ thick and continuous with the wall of the sporogenous filament, being at first clearly distinguished from the very thick, continuous, laminated, 20 – 30μ thick (to 38μ with KOH) endospore. The contents is rather dense and finely granular, or jelly like in appearance, with larger oily bodies here and there. The sporogenous filaments which can sometimes be traced a short distance even from mature spores, seem to be simple and show no signs of any structure which might be regarded as possibly conjugating elements; although it is by no means certain that such organs might not possibly be recognizable in much earlier stages than those which have been examined. Owing to secondary tangential growth of the sporocarp, the spores, as above mentioned, not only tend to become discrete, and to arrange themselves in a single layer; but the spaces in which they lie may become considerably enlarged, so that they may lie in a loculus of considerable size, quite free, or suspended by a few adherent radiating filaments, Figure 92.

The spores, when they have been seen at all, have been variously referred to as asci, perithecia, vesicles or even glands. In very well matured individuals which have been slightly shrunken by alcohol, the position of the spores may be indicated externally, even to the naked eye, by slight corresponding elevations, which have very much the appearance of perithecial ostioles; and it is therefore not so surprising that, in the original description of the type, they should have been spoken of as "pale perithecia filled with hyaline gelatine."

Von Höhnelt in his description, gives the first indication which has been found in the literature, of what appears to be their true nature, and includes what he regarded to be the new genus *Endogonella* among the chlamydosporic types of the *Endogoneae*. Apart from the fact, however, that the plant is described and represented upsidedown, it answers in all particulars to *Glaziella vesiculosa* Berk. There is also absolutely no difference which I have been able to discover, between *Xylaria aurantiaca* B. & C. collected by Wright in Cuba, and Berkeley's type collected in Brazil by Glaziou. It seems quite remarkable,

however, that there appear to be no other synonyms, and that, although several other species of *Glaziella* have been listed, the genus remains monotypic.

A final opinion with regard to its true relationships can hardly be formed until the nature of the primary vegetative and sporogenous hyphae is known. It seems not impossible that, like *Sclerocystis*, it possesses two distinct sets of hyphal elements, the one concerned in sporulation and without septa, the other copiously septate. Although in *Sclerocystis* the septate elements seem to be lysigenous, and are designed to free and scatter the sporocarps and spores; and in the present genus, on the contrary, their object appears to be to hold them firmly in a coherent mass which they render esculent and make conspicuous by raising it above the substratum through a mechanism remotely comparable to that of some phalloids, their ultimate function, namely an effective dispersal of the spores, may be assumed to be the same.

In both genera, the fact that one element in their structure does not conform to the ordinary phycomycetous type, since it is composed of copiously septate filaments, may be explained by their specialization for a definite purpose other than sporulation. In *Sclerocystis* at least, the sporogenous element corresponds in structure to that of the *Mucorales*, since its hyphae are more strictly continuous even than in *Endogone*. Whether this is also the case in *Glaziella* cannot be determined till very young material is available for study. The presence of an independent and continuous endospore, Figure 91, like that of the zygosporoes in *Endogone*, points to a further possibility of their sexual origin.

In any case *Sclerocystis* and *Glaziella* may be assumed to illustrate the highest degree of differentiation which is reached in the family, so far as it is known; and their structure and development is the more remarkable, when it is contrasted with the relatively simple conditions which obtain in other forms. They do not seem, however, to be nearly related, although, if the above suggestion as to the sporogenous element in *Glaziella* is correct, the dual nature of the elements which compose them and the definite segregation of the sporulating regions are characters in common. The wefts of finer filaments which in *Glaziella* are associated with spore-origins which might be regarded as corresponding to the sporocarp initials of *Sclerocystis*, do not, however, seem comparable; since the fine filaments which compose them become closely septate, and seem to arise directly from the inner layer.

It should be mentioned that all other fungi which have been in-

cluded in *Glaziella* appear to belong among the ascomycetes: similarity in color, sterility, and gelatinous consistency having apparently been the only reasons for their inclusion in it. Among these forms the most important is *Glaziella splendens* Cooke (1882), p. 83, described by Berkeley & Curtis (1868) as *Xylaria splendens*, which, like "*Xylaria*" *aurantiaca*, was also collected in Cuba by Wright, is represented in the Curtis collection by one half of the type, the other half, which is figured by Lloyd (1919), p. 29, being in the Kew Herbarium. The Curtis half has been examined and sectioned with some care, and is certainly in no way related to *Glaziella*. Its characters are entirely similar to those of *Entonema liquescens* Möller (1901), p. 247 with figure, and it seems very probable that it may be the sterile condition which appears sometimes to be associated with this species, or at the least an immature stage. It is not hollow, has the same bright granular superficial crust and an inner gelatinous region composed of colorless hyphae with thick soft gelatinous walls, which is subtended by a contrasting black zone or line. There are absolutely no signs of spores or of developing perithecia, and one is inclined to agree with Möller that descriptions of sterile forms of this nature should be disregarded by mycologists.

Glaziella sulphurea Patouillard (1903), p. 292, judging from the description, is certainly not a *Glaziella*, and appears also to correspond very closely with the sterile condition of *Entonema liquescens*.

Glaziella ceramichroa (Berk. & Broome) Cooke (1882) is very surely not of this genus. Mr. Petch assures me that his reference (1910), p. 427, No. 61, of the species to *Hypocrella* is correct.

Glaziella abnormis (Berk.) Cooke (1882), in which asci and ascospores are described, must evidently be excluded; since it also appears to be very near to, if not identical with, *Entonema liquescens*.

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EXPLANATION OF THE PLATES.

DESCRIPTION OF THE FIGURES.

The figures are for the most part camera drawings which have been reduced more than one half in reproduction. Unless otherwise stated the original combination used is Zeiss obj. D and ocular 4, with table projection.

PLATE I.

Endogone pisiformis Lk.

FIGURES 1-5. Successive stages in the formation of zygospores. 1-4, obj. J, oc. 4; 5 obj. J, oc. 2.

FIGURE 6. Mature spores with gametes still attached.

FIGURE 7. Peculiarly differentiated hypha forming the superficial tomentum of a young individual.

Endogone multiplex Thaxter.

FIGURE 8. Mature spore showing hyphal envelope.

FIGURE 9. Mature spore with discrete gamete attachments, treated with KOH.

FIGURE 10. Larger and smaller spore-groups surrounded by envelope with incorporated humus-material.

Endogone tuberculosa Lloyd.

FIGURE 11. Section of sporocarp showing disposition of sporogenous areas, (light), with surrounding and penetrating earthy envelope (dark): magnified about seven times as reduced.

FIGURE 12. Portion of gleba showing spores and pseudoparenchymatous hyphal tissue.

FIGURE 13. Spore showing envelope and origin from gametes. Zeiss J, oc. 1.

FIGURE 14. Fully matured spore with greatly thickened exospore.

FIGURES 15-16. Spores of more elongate type.

Endogone incrassata Thaxter.

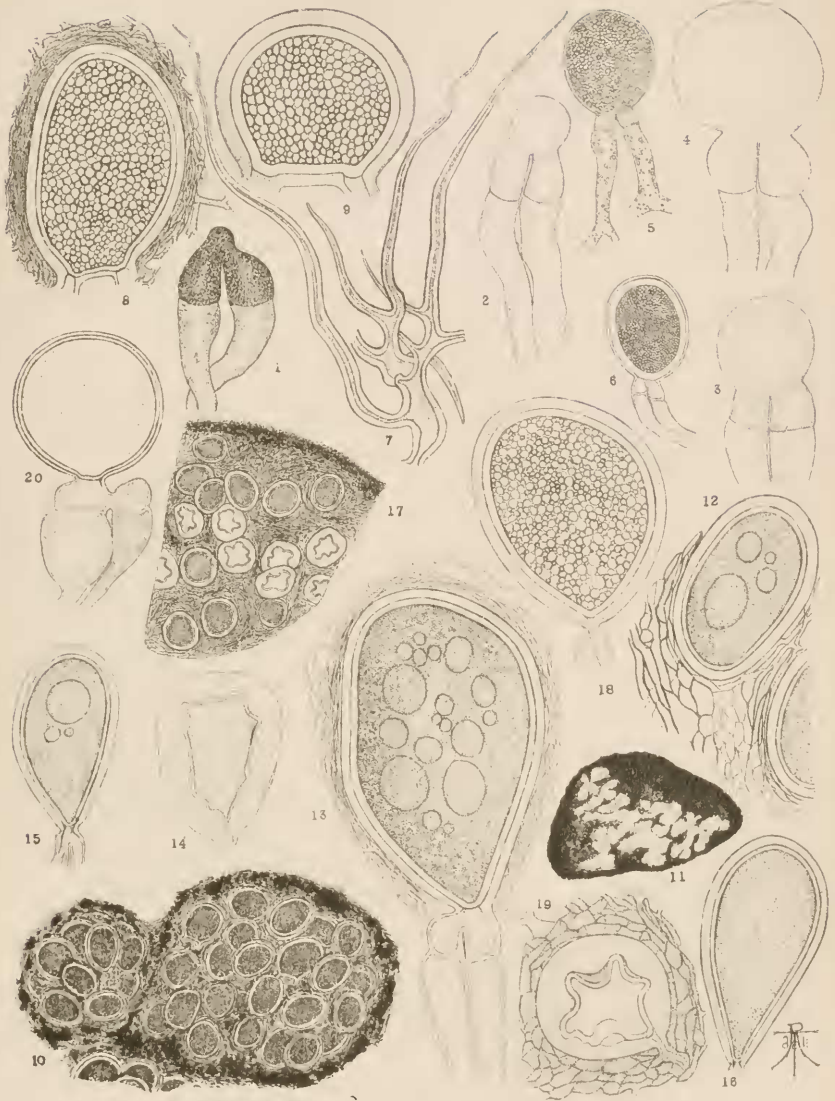
FIGURE 17. Section of a portion of sporocarp, showing peridium and gleba with fully mature and more immature spores.

FIGURE 18. Spore showing characteristic fatty contents and probably sexual origin. Zeiss D, oc. 12.

FIGURE 19. Fully mature spore with greatly thickened exospore and compacted surrounding hyphae.

Endogone lactiflua Berk.

FIGURE 20. Showing origin of zygospore from dissimilar gametes.



THAXTER—REVISION OF ENDOGONEAE

PLATE II.

Endogone fasciculata Thaxter.

FIGURE 21. Sorus of chlamydospores viewed externally. Zeiss obj. A, oc. 4.

FIGURE 22. Section of sorus of chlamydospores showing, above, a few adjacent young zygosporae. Zeiss. obj. A, oc. 4.

FIGURES 23-26. Different stages in the formation of zygosporae. Zeiss obj. J, oc. 2.

FIGURES 27-28. Separated chlamydospores.

Endogone vesiculifera Thaxter.

FIGURE 29. Partial section of a sorus showing origins and association of chlamydospores and thin-walled clavate vesicles. Zeiss obj. A, oc. 4.

FIGURE 30. Clavate vesicles and their origin.

FIGURES 31-32. Separated chlamydospores and their origins.

Endogone fuegiana Spegazzini.

FIGURE 33. Section of gleba showing discrete spore-groups. Zeiss obj. A, oc. 4.

FIGURE 34. Section of single spore-group, showing spore-origins.

Endogone microcarpa Tulasne.

FIGURES 35-37. Chlamydospores from Californian material.

Endogone arenacea Thaxter.

FIGURES 38-40. Three mature chlamydospores with their origins.

Endogone pulvinata Hennings.

FIGURES 41-43. Three chlamydospores from the type material.

Endogone borealis Thaxter.

FIGURES 44-45. Two chlamydospores.

